CONTRIBUTIONS TO THE ICHNOLOGY AND ICHNOFABRICS OF DEEP MARINE SYSTEMS

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By

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Abstract

The new data presented in this thesis demonstrates that detailed palaeoenvironmental reconstructions of deep marine and turbidite settings are improved with the integration of ichnofabric analysis. This thesis is divided into three papers; each using ichnofabric analysis in end-member sedimentological, deep-water systems. In addition, neoichnological research conducted as part of this project links modern and ancient tracemaker behaviour to provide a new model for a commonly observed trend in trace fossil distribution in deep-water settings.

Facies analysis was integrated with ichnofabric analysis in the Eocene/Oligocene sand-rich turbidites of the Grès d'Annot Basin, SE France. Bed-by-bed logging demonstrated that ichnofabric analysis can be used as a high resolution tool for reconstructing depositional palaeoenvironments and their variability in deep-water systems. The *Ophiomorpha rudis* ichnofabric association (analogous to the *Ophiomorpha rudis* ichnosubfacies of the *Nereites* ichnofacies) are present in deposits of high current energy settings and low nutrient levels like channelized sands and thick-bedded turbidites in the Grès d'Annot Basin. The nature of the Grès d'Annot Basin as a thrust sheet-top basin confined and channelled the infilling turbidites. This confining of flows suppressed the deposition of thin-bedded and heterolithic turbidites which allow the preservation of a diverse ichnofauna. Low ichnodiversity (restricted to ichnospecies of *Ophiomorpha* and *Thalassinoides*) result from a combination of nutrient stress and the confined nature of the Grès d'Annot Basin. When thin-bedded heterolithic turbidites are preserved, however, they contain a higher ichnodiversity, density, and abundance of trace

fossils than sand-rich facies. The *Ophiomorpha annulata–Planolites* and *Phycosiphon–Ophiomorpha rudis* ichnofabrics represent the activity of vagile, deposit feeding and farming organisms in quiescent basin slope settings and channel fill facies where turbidites of low erosive power allowed the preservation of a greater number of ichnogenera. This paper is the first ichnologically-based study of Grès d'Annot Basin and demonstrates the utility of ichnofabrics in reconstructing palaeoenvironments and changes in depositional conditions.

Ophiomorpha is commonly observed at sandstone-mudstone interfaces in turbidite systems, including the Grès d'Annot Basin. This paper presents evidence that interface trace fossils represent a deep-sediment farming strategy in deep-water settings with data obtained using mesocosm experiments, CT imagery, and geochemical analyses. The modern thalassinid shrimp *Neotrypaea californiensis* constructs interface burrows morphologically identical to *Ophiomorpha rudis* as observed in the Grès d'Annot (and other) systems. Mesocosms were mapped in three dimensions with CT imagery showing that burrows were preferentially constructed at sand-mud interfaces. The characteristic burrow-lining pellets of *Ophiomorpha* are traditionally considered to be a structural reinforcement to prevent burrow collapse. Our studies have shown that this might not be true in all cases as *N. californiensis* was observed feeding from the pellets indicating they might be a nutritional resource. Geochemical analyses showed higher total organic carbon values in burrow linings and pellets compared to unbioturbated samples from the same mesocosm. Observation showed that *N. californiensis* selected organic carbon-rich grains to make the pellets while higher TOC values indicate organic enrichment with burrow walls having an increased bacterial biomass (with bacterially produced dissolved

organic carbon). Stable isotope analysis showed that the pellets where generally enriched in ^{13}C compared to the isotopically lighter host sediment. This is interpreted as aerobic microbial fractionation. By bioirrigating their burrows *N. californiensis* (and other ancient *Ophiomorpha* tracemakers) encouraged the growth of aerobic microbial populations in burrow-lining pellets which they used as a nutritional resource, utilizing microbial dissolved organic carbon. This new data provides a model for the abundance of trace fossils at sandstone-mudstone interfaces in turbidites systems which had hitherto been unexplained.

The Upper Cretaceous Wyandot Formation, offshore Nova Scotia, is an autochthonous carbonate reservoir facies. This pelagic system was used to demonstrate that ichnofabric analysis can be successfully employed across a range of deep-water palaeoenvironments. The Wyandot Formation is divided into two lithofacies: chalk and marlstone. Ichnofabric analysis showed that the *Chondrites-Thalassinoides-Zoophycos* ichnofabric dominates both lithofacies. High densities and abundances of ichnotaxa in this ichnofabric, in conjunction with a highly bioturbated mixed layer (BI 5-6), imply a well oxygenated sediment-water interface. Environmental perturbations are interpreted through changes to *Chondrites*-dominated ichnofabrics. In the Wyandot Formation this resulted from increased sedimented organic matter, causing the redox front to rise in the sediment, leading to porewater anoxia, and the exclusion of all but the stress-tolerant *Chondrites* tracemaker. This paper successfully tracks changes in the depositional environment of the Wyandot Formation through changes in ichnofabric. A petrographic study of the Wyandot Formation reveals textural and mineralogical differences between burrow fills and host sediment. It is considered that deposit feeding endobenthic

organisms changed the clay mineral assemblages of the sediment by introducing authigenic kaolinite produced during sediment digestion. Burrow fills have a more diverse clay mineral assemblage with a 33% enrichment of kaolinite compared to the host sediment. This is interpreted to be the result of biological weathering and low temperature authigenesis in the digestive systems of the endofauna. This process introduces mineralogical heterogeneity into the Wyandot Formation reservoir facies. This work improves facies analysis and reservoir characterization in an understudied carbonate system.

The work on the Grès d'Annot Basin and the Wyandot Formation presented in this thesis are the first ichnologically orientated studies of these deep-water systems. These data highlight the significance of trace fossil studies in deep-water systems previously understudied with respect to animal-sediment interactions. This thesis also shows that neoichnological research is a useful approach to understanding ancient tracemaker behaviours which can be used to identify palaeoenvironmental conditions. These papers, individually and cumulatively, demonstrate that ichnofabric analysis can be successfully integrated alongside facies analysis in deep-water systems. The trace fossil record can be used to identify changes in depositional and environmental conditions, as well as identifying physiologically stressed conditions on the ancient deep seafloor.

Acknowledgments

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Even though my name is written in big, friendly letters on the cover of this thesis, many friends and colleagues have given their time, effort, and advice to me. I am indebted to my lovely field assistant Steffan Hopcyn-Kitchener for his invaluable work during the 2006 and 2007 field seasons. Steff would like a two page dedication to his hard work in field, but he's not going to get it. Instead he gets the following: thank for letting me drag you up and down Alpine peaks and for carrying our lunch and my samples. I am extremely grateful to my two editors and friends, the Drs Liam Herringshaw and Richard Callow who had no problem telling me what nonsense I might have written. I am very appreciative of Ted DeWitt (U.S. Environmental Protection Agency) for shipping the shrimp (several times) used in the course of this thesis. I count myself very fortunate to have made contact with Ted who was, and still is, willing to send victims. Alfred Uchman is acknowledged for his advice and access to the trace fossil collections at Jagiellonian University, Kraków, Poland, and for very constructive editorial comments on two of the three papers presented herein. Other (outside Memorial University) editorial comments and advice were provided by Denis Lavoie, Trevor Elliott, Andrew MacRae, Andreas Wetzel, John Paul Zonneveld, an anonymous reviewer, and the staff at the CNSOPB. I also thank my external examiner, Luis Buatois (University of Saskatoon) for help in shaping the final draft of this thesis.

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Co-authorship Statement

The following chapters are presented in manuscript format. Each chapter/manuscript has already been, or will be, submitted to an international scientific journal, as indicated at the bottom of each title page. Consequently, these works have involved collaboration with other authors. Taking each in turn, I shall lay out the work personally done and contributions made by my co-authors that helped shape the final drafts. In each case the work is predominantly my own, completed with some guidance and editorial advice from my supervisor and co-author Duncan McIlroy and other junior collaborators.

Chapter 2 is a field-based study, involving ichnological characterization of the Grès d'Annot turbidite system. Field-work was undertaken by myself and involved a four week field season in the summer of 2006 followed by a six week field season in 2007. Both seasons involved extensive field logging of the Grès d'Annot Formation. All data were collected by me (logs, sampling). The logistics and planning of the seasons were also carried out by me. Co-author Dr. Trevor Elliott (independent consultant, Liverpool, UK) has extensive knowledge of the basin and directed me towards good localities to start my field-work and provided insight into the Grès d'Annot Basin. Trevor Elliott met with me in the field on both occasions for one to four days, respectively. Further study areas were located by me. Dr. McIlroy spent a week in the field with me in 2008 reviewing sedimentological and ichnological context and data. I am the primary author on the manuscript with my supervisor Duncan McIlroy and Trevor Elliott providing constructive editorial comments and guidance. This work was funded by an NSERC Discovery Grant and an NSERC/PRAC CRD Grant to Duncan McIlroy, with supplementary funding from the Pan-Atlantic Petroleum Systems Consortium.

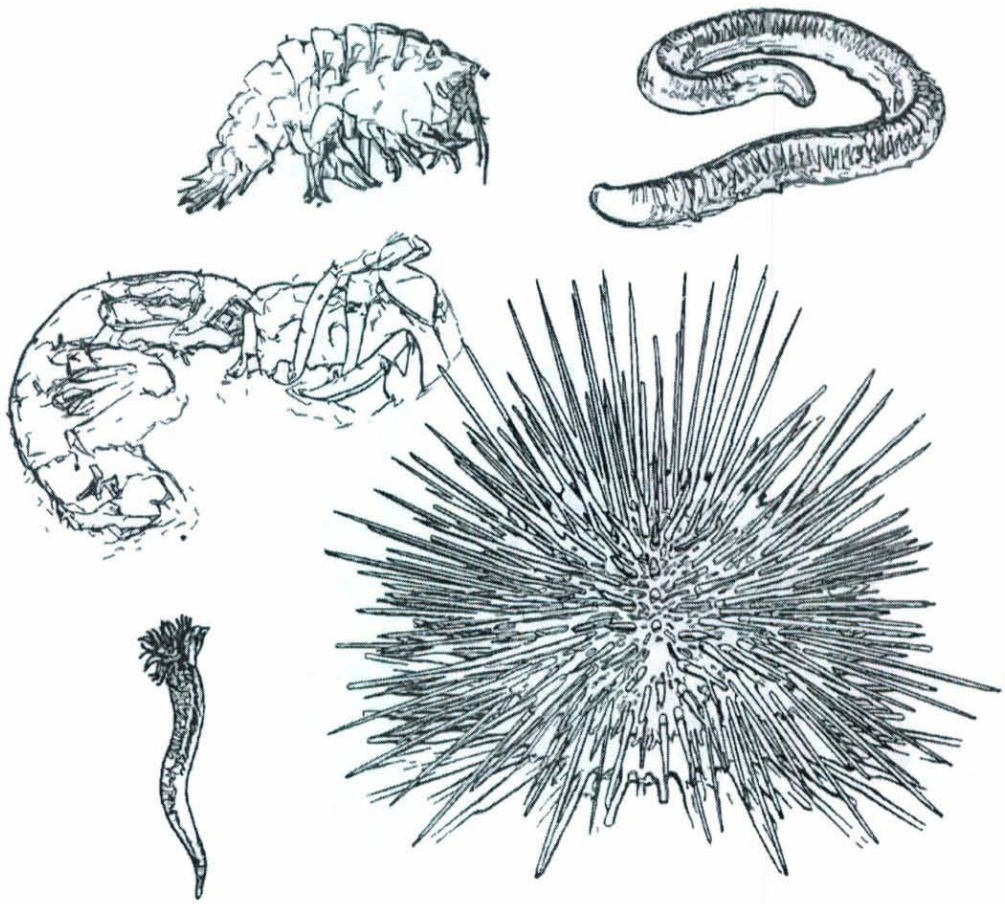
The second manuscript (Chapter 3) involves laboratory-based mesocosm experiments carried out a Memorial University. The aquaria were already in place upon my arrival at Memorial University. The particular mesocosm sediment profiles used in this experiment (detailed in the manuscript) were devised by me. The tracemakers were shipped in from the coast of Oregon, USA. By searching the literature on modern progenitors of *Ophiomorpha* and *Thalassinoides* I made contact with Ted DeWitt (US

Environmental Protection Agency) based in Newport, Oregon, and he agreed to collect, initially, 12 specimens of *Neotrypaea californiensis* and ship them to Newfoundland. I organized the shipment, acquired all necessary licences and permission for a smooth journey for the animals. CT scanning was done by me with aid of Wanda Ayward. Images/slices were digitally altered and, although not an author, Małgorzata Bednarz (a member of the ichnology group at MUN) helped me volumetrically render the stack of images I made to produce a three-dimensional reconstruction of the burrow network using VolView 2.0 (Kitware Inc.). Geochemical analyses were carried out at Memorial University. Sample preparations were done by me, as were the geochemical analyses with initial supervision by Alison Pye (MUN). Duncan McIlroy provided financial support and editorial comments and guidance during construction of the manuscript. Richard Callow (MUN) provided input on tracemaker behaviour at amalgamation surface, the images for Fig. 3.2 (a field locality I did not personally visit), as well as editorial comments during the writing of the manuscript. Liam Herringshaw (MUN) also provided editorial comments. Funding came from a NSERC Discovery Grant and a CRD Grant to Duncan McIlroy.

The third manuscript (Chapter 4) is a core-based study on deep-water chalk deposit from offshore Nova Scotia. This involved logging core at CNSOPB, Dartmouth, Nova Scotia for one week in May 2008. All images logs, images were personally acquired. Andrew MacRae (Saint Mary's University, Nova Scotia) helped me in finding suitable cored intervals through the Wyandot Formation. Thin sections were sent out of Memorial University to be made by Joe Macquaker (then at Manchester University, UK, now at MUN). Petrographic work was personally done at Memorial University with initial supervision of Michael Schaffer and Joe Macquaker on the SEM. Duncan McIlroy provided editorial comments that helped shape the final paper. Funding came from the Pan-Atlantic Petroleum Systems Consortium.

CHAPTER 1

Traces of the deep: an introduction to invertebrate ichnology



CHAPTER 1

Traces of the deep: invertebrate ichnology in deep-sea palaeoenvironments

Aims of this thesis

This thesis describes trace fossil assemblages and ichnofabrics from deep-water palaeoenvironments. In addition, it proposes a model for a commonly observed, but hitherto unexplained, distribution of ichnotaxa in turbidite systems. The ichnological literature has focussed on the description of the trace fossil record in term of ichnofacies (facies-controlled groupings of trace fossils). Although this method has merits, the under-utilized ichnofabric approach has a higher resolution of detail, particularly in the deep marine and turbidite-influenced environments where the broad geographical and geological environments are characterized by only a few ichnofacies. The aims of this thesis are threefold:

1. Turbidite ichnology (and ichnofabrics) will be described from the Eocene/Oligocene siliciclastic deposits of the Grès d'Annot Basin, SE France. This large, and well-exposed, basin can be used as a natural laboratory to highlight the utility of ichnofabric analysis in deep marine palaeoenvironments and allows for more refined facies interpretations of turbidite systems. This paper links facies analysis to ichnofabric analysis in different environments in the Grès d'Annot turbidite system. It seeks to show how ichnofabric analysis can be used

to interpret environmental changes and decipher depositional conditions in a turbidite system understudied with respect to ichnology.

2. Burrows along sandstone-mudstone interfaces are common in the geological record of turbidite systems (including the Grès d'Annot Basin). In this paper a model will be proposed to explain this trace fossil distribution. Mesocosm experiments, CT imagery, and geochemical analyses are used to provide data to support the hypothesis that the preference for burrows along sandstone-mudstone interfaces in ancient deep-water settings is related to a deep-sediment feeding strategy.
3. The Upper Cretaceous Wyandot Formation, offshore Nova Scotia, is an understudied reservoir facies. It will be used for refining models of chalk deposition (and analogous sediments). Wells drilled through the Wyandot Formation will be examined and the ichnofabric method employed to reconstruct the depositional environment and identify any depositional or environmental changes. A petrographic study of the Formation will also be undertaken to examine whether infauna produced a change in the texture and mineralogy of the Wyandot sediment and if this impacts reservoir quality. This study will improve facies analysis and reservoir characterization for deep-water (pelagic) palaeoenvironments.

1.1. Introduction and overview

Prior to the 19th century the technological challenges of studying the deep seafloor were too great to be overcome. It was considered to be a dark and barren plane devoid of life often described as a 'deep-sea desert' (Uchman, 2007). The first scientific studies of the deep sea dredged up homogeneous mud from each station while noting that deep-water taxa displayed similar morphologies and behaviours to their shallow-water counterparts (Maury, 1857). Greater advances came with the research conducted on board the H.M.S. *Challenger* on its 1872 expedition, sampling the ocean floors and cataloguing numerous taxa. Our understanding of the deep sea has increased further in recent years with deep-water exploration undertaken by the Ocean/Deep-Sea Drilling Project along with advances in technology like deep-sea submersible vehicles. Photography of ocean floors and recovery of box cores have revealed numerous surface and in-sediment structures such as burrows, ridges, grooves, tracks, trails, and faecal strings of worms, echinoids, bivalves, and holothurians (Heezen & Hollister, 1971; Hollister *et al.* 1975; Ekdale & Berger, 1978; Ekdale, 1980; Gaillard, 1991). The resemblance of these modern deep-sea biogenic structures to trace fossils in ancient settings is clear. Even with these advances, our knowledge and understanding of the deep sea are lacking compared with shallow and coastal marine environments (Gage, 1996). This thesis will investigate ancient deep-sea sediments, and using trace fossils, improve our understanding of these environments, sedimentary processes, and their effect on the benthic community.

Before this work begins in earnest it is necessary to provide some definitions for the key terms frequently used and to provide a framework for the ideas and results presented herein. *Ichnology* is the study of trace fossils, bioturbation, and animal-sediment interactions in the rock record (e.g. ancient examples of the life-processes of organisms; Häntzschel, 1975; Bromley, 1996; Bertling *et al.* 2006). *Neoichnology* is the study of modern biogenic structures and bioturbation in the field or laboratory (Bromley, 1996). Neoichnological studies have revealed modern examples of many trace fossil genera in deep-water environments (Ekdale & Berger, 1978; Ekdale, 1980; Wetzel & Werner, 1981; Wetzel, 1983, 2002; Gaillard, 1991; Wetzel & Bromley, 1994). Trace fossils in ancient and modern deep-sea settings have been explored by numerous authors (Seilacher, 1962, 1964, 1977; Wetzel, 1983, 1984; Uchman, 1995, 1998, 2001; Savrda & Bottjer, 1989a, 1989b; Mángano & Buatois, 1996; Buatois *et al.* 2001, 2009) but studies incorporating ichnofabric with facies analysis are lacking. This thesis uses ichnofabric analysis to document ancient deep-water environments and shows how trace fossil are important biosedimentary structures that can identify changes in the depositional and environmental conditions on the deep seafloor. Case studies presented in this thesis include examination of the Grès d'Annot Basin, SE France (a turbidite system in Chapter 2) and the Wyandot Formation, offshore Nova Scotia (an autochthonous pelagic chalk deposit in Chapter 4). The neoichnological study employed in this work proposes a reason for a hitherto unknown distribution of trace fossils in deep-water palaeoenvironments (Chapter 3).

The current definition of a *trace fossil* encompasses all biosedimentary structures resulting from the life activity of an organism (or homotypic organisms) preserved in a

sedimentary or lithified substrate (Häntzschel, 1975; Bertling *et al.* 2006). Structures classified as trace fossils include fossil burrows, borings, tracks and trackways, coprolites, gastroliths, regurgitaliths, nests, woven cocoons, spider webs, leaf mines, and bite and gnaw marks (Bertling *et al.* 2006). Morphologically recurring characteristics allow the classification of trace fossils into *ichnogenera*, suggesting that the trace fossils grouped within an ichnogenus were made by organisms exhibiting similar behavioural strategies (Bromley, 1996; McIlroy, 2004a). Trace fossils within an ichnogenus that have identifiable morphological variations related to differences in tracemaker behaviour allow the description of an *ichnospecies*. Ichnological taxonomy (ichnotaxonomy) is governed by the principles and guidelines defined by the International Code of Zoological Nomenclature (ICZN) which applies zoological nomenclature to these structures. The latest edition of the ICZN embraced the concept of ichnotaxonomy with the formal establishment of ichnogenera and ichnospecies levels (ICZN, 1999; see discussion in McIlroy, 2004a).

Bioturbation is the process of sediment mixing, laterally and vertically, by epibenthic animals (those which live on the sediment surface) and endobenthic animals (those that live within the sediment). Bioturbation results in the disruption of primary sedimentary fabric, the formation of biogenic sedimentary structures (trace fossils), and a biologically modified fabric that may enter the rock record (as an ichnofabric; see discussion below for definition of ichnofabrics). The degree of bioturbation, the *bioturbation index (BI)*, can be quantified by comparing the amount of biogenic fabric relative to the primary sedimentary fabric (Droser & Bottjer, 1986; Goldring, 1995; Table 1.1). This can be displayed visually in an ichnofabric constituent diagram (or ICD; Goldring, 1993; see Fig.

BI	Percentage Bioturbation	Description
0	0	No bioturbation. All primary sedimentary fabric preserved.
1	1-5	Sparse bioturbation: a few discrete traces and /or escape structures.
2	6-30	Low bioturbation: bedding distinct, low trace diversity, escape structures common.
3	31-60	Moderate bioturbation: bedding boundaries sharp, traces discrete.
4	61-90	High bioturbation: bedding boundaries indistinct, high trace density with overlap common.
5	91-99	Intense bioturbation: bedding completely disturbed, limited reworking due to repeated
6	100	Complete bioturbation: burrow homogenized sediment due to repeated overprinting.

Table 1.1. The bioturbation index (BI) describing the degress of sediment disruption by benthic organisms relative to the primary sedimentary fabric. Modified from Taylor *et al*. (2003).

2.3 in Chapter 2 for examples of deep-water ICDs). The fossil record of a single endobenthic community of a contemporaneous group of animals is called an *ichnocoenosis* (Davistashvili, 1945; Lessertisseur, 1955; Häntzschel, 1975). Ichnocoenoses can be identified by ichnofabric analysis and cross-cutting relationships between trace fossils recording the burrowing activity of generations of time-averaged bioturbating organisms (McIlroy, 2004a).

Trace fossils are useful biogenic structures for geoscientists undertaking palaeoenvironmental analysis. They are autochthonous structures that reflect behavioural responses to depositional and palaeoenvironmental conditions at the time of formation (Bromley & Ekdale, 1986; Taylor *et al.* 2003; MacEachern *et al.* 2007a). Trace fossils can be used in numerous disciplines including: (1) palaeoenvironmental studies aimed at identifying stressed conditions on the deep-sea floor (Chapters 2 & 4; Wetzel, 1984, 2010; Savrda & Bottjer, 1986, 1989b; Uchman, 2004; MacEachern *et al.* 2007b); (2) identifying surfaces of stratigraphic significance (Savrda, 1991, 1995; Ghibaudo *et al.* 1996; MacEachern *et al.* 2007a); and (3) petroleum-related studies where biogenic structures influence the porosity and permeability of reservoir units (Chapter 4; Gingras *et al.* 1999, 2007; Pemberton & Gingras, 2005; Tonkin *et al.* 2010).

1.2. The effects of bioturbation on the sedimentary environment

Organisms and their environment are closely linked. These interactions have been well-studied in benthic marine environments (Rhoads, 1974; Aller, 1978, 1982; Dufour *et al.*

2008; Herringshaw *et al.* 2010). The presence of an organism within a sediment column changes the physical and chemical properties of that sediment (Wetzel & Uchman, 1998a). This is especially evident for deposit feeding organisms that live entirely in the sediment (Gingras *et al.* 2008). Bioturbation affects the host sediment at a variety of scales, from the manipulation of individual grains, to the modification of the whole sediment profile. The geotechnical and geochemical modification of sediment properties by benthic organisms are discussed below.

1.2.1. Geotechnical modifications

Without bioturbation, primary sedimentary fabric can be preserved (excepting the effects of loading and soft sediment deformation). Burrowing organisms modify the sedimentary fabric by moving through the substrate, constructing burrows, and feeding within the substrate (Brenchley, 1981; Wetzel & Uchman, 1998a; Mermillod-Blondin *et al.* 2004). The main physical effects resulting from bioturbation are: (1) the redistribution of sedimentary particles, affecting sediment sorting (Warme, 1967; Howard, 1975; Ziebis *et al.* 1996; Herringshaw *et al.* 2010); (2) an increase or decrease primary sediment permeability and porosity (e.g. Gingras *et al.* 1999; Pemberton & Gingras, 2005; Tonkin *et al.* 2010); and (3) changes in substrate stability such as binding previously unconsolidated material or destabilizing previously consolidated material (Rhoads & Young, 1970; Nowell *et al.* 1981).

1.2.1.1. Sediment redistribution

Mixing and sorting of sedimentary particles by benthic animals disrupts or removes primary bedding and lamination. The thalassinid crustacean *Neotrypaea californiensis* (formerly *Callianassa californiensis*) redeposits sediment from depth in the substrate onto the surface during burrow excavation (Miller, 1984). At Mugu Lagoon, California, *N. californiensis* are found in densities of over 100 m^{-2} and are calculated to rework 20-50 cm^3 of sediment per day (MacGinitie & MacGinitie, 1949). Consequently, a community of *N. californiensis* can deposit 1-3 m of structureless sediment onto the surface per year (Miller, 1984; Miller & Myrick, 1992). Likewise shrimps of the genus *Callianassa* dump sediment at the sediment-water interface where finer grains are winnowed away by currents, leaving a coarser sediment profile (Shinn, 1968). Active selection and ejection of fine-grained material has been observed by the mud shrimp *Callianassa truncata* leading to improved sediment sorting (Ziebis *et al.* 1996). These behaviours lead to biologically induced sediment grading (normally graded) or the loss of all primary sedimentary structures (Warme, 1967; Macquaker & Howell, 1999; Richardson *et al.* 1983, 2002).

Benthic animals have numerous methods of burrowing (moving sediment up, down, and laterally) and employ a wide range of feeding strategies (Bromley, 1996; Bentley *et al.* 2006). Head-down deposit feeders, like some polychaete worms, feed at depth in the sediment, and with their anus close to the sediment-water interface, expel faecal material onto the sediment surface (Fauchald & Jumars, 1979; Bromley, 1996; François *et al.* 1997; Herringshaw *et al.* 2010). Taking fine-grained material from depth and expelling it at the surface changes the grain-size distribution of the sediment

producing coarser, cleaner sediment at the bottom of the bioturbated zone (Bentley & Nittrouer, 2006; Dufour *et al.* 2008; Tonkin *et al.* 2010). Conversely, head-up feeders take fine-grained material from the surface and expel it at depth in the sediment (François *et al.* 1997) or can incorporate it into burrow walls (Herringshaw *et al.* 2010). Either way, benthic animals change the grain-size distribution of the sediment profile by actively moving finer-grained material during feeding and burrowing activities.

Meiofauna can alter the sediment profile by manipulating individual grains by their feeding and migratory behaviour (Howard & Frey, 1975; Pemberton & Gingras, 2005). This process is called cryptobioturbation and involves the movement (by ingestion or mechanical manipulation) of selected sediment grains over short distances (Howard & Frey, 1975; Bromley, 1996). Meiofauna such as nematodes and copepods have been observed to migrate 25 cm during a tidal cycle resulting in physical disturbance of the sediment (Reichelt, 1991). This results in 'fuzzing' of the sedimentary fabric and may eventually lead to homogenization of the bioturbated unit or production of cryptobioturbation (Pemberton *et al.* 2008). Bulk sediment processing involving large numbers of highly mobile deposit feeding endobenthic organisms is perhaps the most effective way of bioturbating sediment. Deposit feeders are estimated to be able to move 10-100 times more sediment than suspension feeders over the same time period (Gingras *et al.* 2008). As a result deposit feeders have a greater impact on ichnofabric production, per individual, than suspension feeders (McIlroy, 2007).

1.2.1.2. Permeability and porosity

Bioturbating organisms construct vertical and horizontal burrows as well as burrow galleries in the sediment (Bromley, 1996). These burrows are passively or actively filled by the tracemaker resulting in textural heterogeneities that alter the bulk permeability and porosity of the sediment or rock (Gingras *et al.* 1999, 2002, 2004, 2007; Pemberton & Gingras, 2005; Pemberton *et al.* 2008; Tonkin *et al.* 2010). Biogenically enhanced permeability can be achieved by many different permutations of burrow form and morphology (Pemberton & Gingras, 2005; Tonkin *et al.* 2010). Bulk permeability of the sediment is affected by sediment reorganization techniques employed by benthos and described above (e.g. biologically improved sorting by ejection of fines; Ziebis *et al.* 1996). Large communities of the lugworm *Arenicola marina* were found to improve sediment permeability and sorting by ejecting fine-grained material from their burrows (Volkenborn *et al.* 2007). Burrows made in firm substrates such as dewatered or compacted muds can be passively infilled by a coarser and more permeable material (Pemberton & Frey, 1985). This textural heterogeneity between burrow fill and host sediment allows enhanced permeability pathways in otherwise impermeable, firm, and commonly fine-grained substrate (Gingras *et al.* 2004, 2007). As a result of their impact on permeability and porosity trace fossils are gaining recognition for the role they play in enhancing reservoir quality (Gingras *et al.* 1999, 2007; Pemberton & Gingras, 2005). It is also important to note, however, that bioturbation can have an adverse effect on sediment permeability (Tonkin *et al.* 2010). Sediment packers (those that place fine-grained material into burrow walls, like the tracemakers of *Ophiomorpha*) have been found to

locally reduce permeability and porosity by 33%, having a deleterious effect on reservoir quality (Tonkin *et al.* 2010).

1.2.1.3. Substrate stability

Burrowing animals are able to both bind and destabilize the substrate (Rhoads & Young, 1970; Eckman *et al.* 1981; Nowell *et al.* 1981). Burrowing can reduce grain-size sorting and introduce porewater into the sediment leading to reduced cohesion of sedimentary grains, increased water content, and an increased chance of resuspension by bottom currents (Rhoads, 1970; Nowell *et al.* 1981). Bioturbation can decrease sediment stability by increasing seafloor roughness through increasing the effective grain-size (Eckman *et al.* 1981; Volkenborn *et al.* 2007). Benthic animals can increase effective grain-size by the biodeposition of faecal pellets (Snelgrove *et al.* 2001). By increasing surface roughness, burrowing organisms increase the boundary shear stress and decrease the critical entrainment velocity for sedimentary particles and faecal pellets at the sediment-water interface (Nowell *et al.* 1981). Faecal pellets increase surface roughness and so are easily resuspended and transported as bedload (Nowell *et al.* 1981; Bentley & Nittrouer, 1999). Deposit feeders at or near the sediment-water interface cause sediment destabilization by the resuspension and redeposition of fine-grained material (Rhoads & Young, 1970). This limits the settlement of some benthos, particularly planktonic larvae (Rhoads & Young, 1970; Meadows & Meadows, 1991). Conversely, bioturbation can enhance the stability of the substrate through initial colonization by tube builders (Rhoads & Young, 1970). Polychaetes have been found to bind sediment particles together with mucous, stabilizing their burrows and the surrounding substrate (Rhoads, 1970; Meadows

et al. 1990; Dufour *et al.* 2008; Herringshaw *et al.* 2010). This is evident in high density populations of the tube-building polychaete *Melinna cristata* (5000 m^{-2}) where they were found to bind soft, silty substrate (Buchanan, 1963; Fauchald & Jumars, 1979). By encouraging the growth of bacteria and algae, tube-builders are indirectly responsible for sediment binding by microbial mucous (Eckman *et al.* 1981). Experiments have also shown that the byssal threads of mussels also act to increase sediment stability in dense populations (Shand, 1991).

1.2.2. Geochemical modifications

Bioturbation by micro-, meio- and macrofauna can alter the geochemistry of the substrate and modify the influx and efflux of nutrients, oxygen, and other dissolved species across the sediment-water interface and burrow walls (Berner, 1980; Aller, 1978, 1982; Kristensen, 2000; Marinelli, 1994; Zorn *et al.* 2006; Herringshaw *et al.* 2010). The construction of burrows and their active ventilation (bioirrigation) alters the supply of oxygen and nutrients to bacteria in the sediment affecting the distribution of geochemical and microbial zonations and reactions (Chapter 3; Aller, 1982; Mermillod-Blondin *et al.* 2004).

1.2.2.1. Bioirrigation

Under steady-state conditions the ocean floor has a geochemical stratification related to microbial respiratory processes within the substrate (Froelich *et al.* 1979; Berner, 1980, 1981; Aller, 1982; Bender & Heggie, 1984; Aplin, 2000). The distribution of these

geochemical zones is affected by the biologically modified flux of oxygen and reductants into the sediment (Aller, 1978, 1982; Ziebis *et al.* 1996; D'Andrea *et al.* 2002). Burrows, whether they are simple vertical tubes such as *Skolithos* or dense maze-type gallery networks like *Thalassinoides*, always act to increase the oxygen flux into the sediment (Zorn *et al.* 2006). Higher densities of burrows are linked to a higher flux of oxygen into the near-burrow porewater system (D'Andrea & DeWitt, 2009). The burrow wall is a site of solute, nutrient, and oxygen exchange between the substrate and water column (Vaugelas & Buscail, 1990; Glud *et al.* 1994; DeWitt *et al.* 2004). Although the burrow wall may be more complex (containing microbial populations and mud-linings) it is analogous to the sediment-water interface and can be thought of as an extension of this surface beneath the sediment (Aller, 1982; Griffis & Suchanek, 1991; Kristensen, 2000). Many endobenthic animals reside in permanent burrows which require ventilation to ensure sufficient oxygenation for respiration (Chapter 3; Farley & Case, 1968; Thompson & Pritchard, 1969; Aller, 1982). Suspension feeders, like some polychaetes, capture plankton for nutrition by bioirrigation (Fauchald & Jumars, 1979). Bioirrigation has been observed in numerous field and laboratory studies (Forster & Graf, 1992, 1995; Marinelli, 1994; Ziebis *et al.* 1996; Aller & Aller, 1998; Kristensen, 2000; Furukawa *et al.* 2001; Zorn *et al.* 2006; and by *Neotrypaea californiensis* in the mesocosm experiments described in Chapter 3). During bioirrigation, animals pump oxygenated water through their burrows, increasing the oxygen flux into the sediment and removing toxic metabolites which builtd up through respiratory processes and excretions (Hines & Jones, 1985; Marinelli, 1994). The modification of oxygen penetration gives rise to a complex geochemical mosaic within the substrate as illustrated by Aller (1982). Active

bioirrigation by a community of the thalassinid shrimp *N. californiensis* was found to increase the depth of the oxygenated zone of the sediment and depress the redox boundary by over 40 cm (Miller, 1984). Mixing the sediment by benthic organisms can also increase the zone of oxygenated sediment (Reimers *et al.* 1986). By repackaging sedimentary grains (as faecal pellets) and re-depositing them in the sediment, head-up feeders change local geochemistry (Aller, 1982). This biodeposition alters the geochemical gradients by acting as a locus for microbial decomposition (Aller, 1982; Kristensen, 2000).

1.2.2.2. Biological weathering

Deposit feeders ingest sedimentary particles either selectively or non-selectively and defecate either on or within the sediment and so affect the texture and geochemistry of the substrate (Fauchald & Jumars, 1979; Jumars *et al.* 1990; McIlroy *et al.* 2003). Bacterial mineralization, alteration of clay mineral assemblages, and clay mineral authigenesis is thought to be a common process (Konhauser & Urrutia, 1999). The passage of clay minerals through an acidic and microbe-rich microenvironment (e.g. the digestive system of a deposit feeding animal) can also have an effect on the mineralogical assemblage of the sediment (Chapter 4; McIlroy *et al.* 2003). Clay mineral assemblages in the faecal pellets of *Callichirus major* (formerly *Callianassa major*) where found to be altered from the suspended clay material initially ingested (Pryor, 1975). Egested sediment grains have also been found coated with clay mineral rims formed by mineral dissolution and precipitation within a deposit feeding organism's gut (Needham *et al.* 2005; Herringshaw

et al. 2010). Consequently, bioturbation and biological weathering can result in mineralogical and textural changes in the sediment (Chapter 4; McIlroy *et al.* 2003).

1.3. Environmental controls on bioturbation

The presence of a single burrowing organism or a whole community of benthic organisms can have a significant effect on the sedimentary environment (see above). Conversely, environmental conditions have a control on the life processes of burrowing organisms and therefore influence trace fossil distribution and ichnofabric preservation (Savrda & Bottjer, 1986; Goldring, 1995; Wetzel & Uchman, 1998a, 1998b; Bentley *et al.* 1996; Uchman, 2004; Dashtgard *et al.* 2008).

1.3.1. Oxygen

Oxygen is one of the primary controls on the distribution of trace fossils and their progenitors (Frey & Seilacher, 1980; Bromley & Ekdale, 1986; Savrda & Bottjer, 1987; Leszczyński, 1991). In persistently anaerobic conditions (< 0.1 ml l^{-1} dissolved oxygen) metazoans are unable to survive (i.e. there is no bioturbation) so primary sedimentary fabrics can be preserved (Savrda & Bottjer, 1987; Macquaker & Gawthorpe, 1993; Wetzel & Uchman, 1998b). In the absence of bioturbation and when the flux of organic matter is high, dark, organic carbon-rich, laminated mudstones can be preserved in deep-water settings (e.g. Savrda & Bottjer, 1989a; Föllmi & Grimm, 1990; Wetzel, 1991a;

Macquaker & Gawthorpe, 1993). Changes in bottom water and porewater oxygenation can be recorded as stratigraphic changes in the trace fossil community (e.g. changes in burrow size, depth of penetration, cross-cutting relationships, density and abundance of trace fossils; Savrda & Bottjer, 1987, 1989b; Ekdale & Mason, 1988; Wetzel, 1991b; Savrda, 1995; Uchman, 2004). Decreased bottom water oxygenation on the deep-basin floor is accompanied by a concomitant shift in the benthic community to smaller, less abundant, simpler burrows and decreased ichnodiversity (Savrda & Bottjer, 1986, 1987; Leszczyński, 1991; Savrda, 1995; Bentley & Nittrouer, 1999). Decreasing oxygenation has been interpreted as the primary cause of changes in assemblages dominated by dwelling burrows (well-oxygenated) to assemblages dominated by feeding and grazing burrows such as *Chondrites* and *Zoophycos* (Ekalde & Mason, 1988; Burton & Link, 1991; Wetzel, 1991b). A decrease in oxygenation can also change the infaunal tiering in a substrate (Ekdale & Bromley, 1984; Wetzel, 1991b). Lowered oxygen levels at the sediment-water interface reduce the depth of oxygen diffusion into the porewater system (Gehlen *et al.* 1997). This leads to a decrease in the depth of the mixed layer and a decrease in the penetration depth of burrowers (Froelich *et al.* 1979; Savrda & Bottjer, 1986, 1989a; Wetzel, 2010).

Chondrites is a common component of ichnofabrics developed in oxygen-deficient palaeoenvironments (Bromley & Ekdale, 1984; Savrda & Bottjer, 1989a; Burton & Link, 1991; Wetzel & Uchman, 2001). The *Chondrites* animal is a deep-burrowing organism commonly responsible for deep-tier trace fossils (Ekdale & Bromley, 1991; Wetzel & Uchman, 1998a, 1998b). The tracemaker is considered to be able to survive in anoxic sediments below the redox boundary while maintaining an open connection to the

sediment-water interface (Ekdale & Mason, 1988; Wetzel, 1991b; Ekdale, 1992; Wetzel & Uchman, 2001). The *Chondrites* animal has been inferred to have a chemosymbiotic relationship with sulfide-oxidizing bacteria which oxidize hydrogen sulfide in the presence of an oxygenated burrow providing dissolved organic carbon (DOC) for its host (Fu, 1991). This gives the *Chondrites* animal a competitive advantage in low oxygen environments. Chemosymbiosis is observed in modern fauna such as bivalves which live close to, or below, the redox boundary (Seilacher, 1990; Dufour & Felback, 2003) and in vent faunas on abyssal plains (Grassle, 1985; Jannasch & Mottl, 1985). When *Chondrites* is present in mono-generic assemblages it has been used to infer lowered bottom water oxygenation at the sediment-water interface and within the sediment (Bromley & Ekdale, 1984; Savrda & Bottjer, 1986, 1987; Wetzel, 1991b).

Turbidity currents can introduce oxygenated water to deep, distal basins (Scholkovitz & Soutar, 1975) providing periodic environmental amelioration and conditions suitable for greater colonization by metazoan life (Leszczyński, 1991). The appearance of bioturbation in previously unbioturbated sediment has been linked to increased oxygenation associated with turbidity current deposition in deep marine palaeoenvironments (Föllmi & Grimm, 1990; Grimm & Föllmi, 1994; Mángano & Buatois, 1997). Oxygenated turbidity currents can also deepen the redox boundary in deep-sea sediments (Wilson *et al.* 1986; Thomson *et al.* 1987; Meyers *et al.* 1996). As oxygenation increases at the sediment-water interface, so the thickness of the bioturbated zone also increases (Savrda & Bottjer, 1987), and the diversity and abundance of trace fossils similarly increase (Burton & Link, 1991; Mángano & Buatois, 1997). Fully oxygenated and stable seafloor settings are commonly linked to high biological and

behavioural diversity and an abundance of benthic organisms and trace fossils (Ekdale & Mason, 1988, Leszczyński, 1991). Seasonal availability of oxygen in some basins can keep the benthic community in the pioneering stage of colonization (Rhoads & Boyer, 1982; Bentley *et al.* 1996; D'Andrea *et al.* 1996). Evidence for fluctuations in bottom water oxygenation (not necessarily seasonal) is common in the geological record (Savrda & Bottjer, 1989; Leszczyński, 1991; Grimm & Föllmi 1994). Deep-sea life and the trace fossil community are sensitive to changes in oxygenation. These changes in the benthic community (preserved as oxygen-related ichnocoenoses and ichnofabrics) can serve as ichnological proxies for changes in deep-sea bottom water oxygenation in ancient settings (Bromley & Ekdale, 1984; Savrda, 1995; Uchman, 2004).

1.3.2. Nutrient supply and sedimentation rate

The modern deep seafloor is typically a nutrient-limited environment (Gooday & Turley, 1990). Most of the organic matter on the seafloor originates from the photic zone delivered in the form of macroscopic aggregates of phytoplankton and faecal pellets (Macquaker & Adams, 2003; Macquaker & Bohacs, 2007; Macquaker *et al.* 2010), and macrobiotic carcasses (Gooday & Turley, 1990). Organic matter may also be delivered to distal basins by turbidity currents, which may carry organic carbon-rich sediments (Wilson *et al.* 1986; Buckley & Cranston, 1988; Wetzel & Uchman, 2001). Under steady-state pelagic conditions (non-turbiditic) the amount of organic matter reaching the seafloor is dependent upon the sedimentation rate (Wetzel, 1983, 1991b), primary productivity, detritivorous nutrient cycling in the photic zone (Logan *et al.* 1995), and the

depth and oxygenation of the water column (Ekdale *et al.* 1984; Wetzel & Uchman, 1998b). Only 1-10% of the organic material that leaves the photic zone is delivered to the seafloor (Suess, 1990) with 95% of remineralization taking place by oxygen oxidation (Bender & Heggie, 1984). Consequently, an increase in the amount of organic matter typically leads to: (1) an increase in the diversity and abundance of the benthic community (Chapter 4; Moore & Dymond, 1988); (2) an increase in the size of burrowing organisms, burrows, and trace fossils (Wetzel, 1981, 2010); (3) an increase in the metabolic activity in the upper layers of sediment (Wilson *et al.* 1985); and (4) lowered oxygen flux into the sediment as microbial respiration uses free oxygen mineralizing organic carbon (Gehlen *et al.* 1997). If remineralization rates are constant then increased sedimentation rates result in increased burial of organic matter (Müller & Suess, 1979). The depth of the bioturbated zone is, to a certain extent, dependent on the amount of organic matter in the sediment column and has been observed to increase with more available organic matter (Wetzel, 1991b; Wetzel & Uchman, 1998b). Values of 0.2-0.4% TOC (total organic carbon) are recorded form modern deep-sea surface sediments (Wetzel, 1982, 1983). Converse to the proliferation of benthos stated above, continued deposition of organic carbon-rich sediments can decrease the abundance and diversity of benthos within the sediment (Chapter 4). Microbial respiration can deplete free oxygen in the sediment during the remineralization of organic carbon resulting in a rising of the redox boundary, porewater anoxia, and the exclusion of most endofauna (as observed in the Wyandot Formation; see Chapter 4; Reimers *et al.* 1986; Wetzel, 2010). Unless an animal lives at depth in the sediment exploiting surface nutrients, or cultivating microbes (see Chapter 3), then there is no advantage to penetrative sediment exploration under low

sedimentation rates. The net effect is that deep burrows are rare (Wetzel & Uchman, 1998b). Surface-grazing trace fossils dominate the ichnofabrics produced under conditions of pelagic mudstone deposition (Wetzel & Uchman, 1998b, Wetzel, 2002). Stratigraphic intervals where sedimentation rates are less than bioturbation rates can be identified by continuous overprinting of burrows (Chapter 4; Ekdale & Bromley, 1983, 1984). This is best exemplified in modern deep-sea successions where the rate of sediment accumulation is greatly exceeded by the rate of bioturbation (Ekdale & Bromley, 1983, 1984). Complete burrow homogenization of primary physical sedimentary fabrics (the removal of primary sedimentary structures by benthic organisms) is common in modern deep-sea pelagic oozes (Ekdale & Bromley, 1984).

Just as seasonality in oxygenation can influence the community structure on the seafloor (Bentley *et al.* 1996), seasonality in nutrient supply can also affect benthos (Quijón *et al.* 2008). Summer blooms of phytodetritus typically stimulate macrobenthic productivity (Quijón *et al.* 2008), and trigger the onset of reproductive cycles which increase the abundance of benthic life and larvae (Gooday & Turley, 1990). Nutrient-deficiency in the deep sea can lead to miniaturization of fauna with a tendency towards selective feeding on individual organic sedimentary particles rather than bulk sediment processing (Jumars *et al.* 1990; Gage, 1996). These behaviours are indicative of the *Nereites* ichnofacies, a deep-water ethological grouping of endobenthos (discussed in more detail below). This feeding strategy is employed by many deep-water fauna including the progenitors of the graphoglyptid group trace fossils (Seilacher, 1977; MacEachern *et al.* 2007c). These geometric-patterned burrows are produced by benthic organisms either microbe farming or trapping microbes or particulate matter, efficiently

exploiting low nutrient sediments in deep-water settings with low pelagic or hemipelagic sedimentation rates (Seilacher, 1977; Ekdale, 1980).

1.3.3. Substrate

Substrate stability defines how a burrow is constructed and affects its preservation potential (Goldring, 1995). In soupground substrates, tracks, trails, and burrows of organisms are misshapen beyond recognition (Chapter 4; Ekdale *et al.* 1984). This poor preservation potential is commonly reflected in low trace fossil diversity (Dashtgard *et al.* 2008). Some organisms, such as amphipods, prefer this type of environment as they move by 'swimming' through the waterlogged sediment (Bromley, 1996). Most animals, however, prefer firmer substrates as they allow the construction of semi-permanent or permanent burrows (Bromley, 1996). Most of the benthic deep marine is softground which is firm enough to allow the construction of open burrows lined with mucus without significant risk of burrow collapse (Wetzel & Uchman, 1998a). In a neoichnological study of marginal marine deposits it was found that firm sand and mud provided the substrate for the highest diversity and abundance of burrows (Dashtgard *et al.* 2008). This high biological diversity is related to the cohesive strength of the substrate allowing permanent burrows to be constructed (Dashtgard *et al.* 2008). Muddy substrates are characterized by larger diameter burrows than in sandy substrates when burrowed by the thalassinid shrimp *Neotrypaea californiensis* (Griffis & Chavez, 1988).

Firmgrounds can be formed by dewatering and compaction of sediment during burial (which may be exhumed by turbidites in deep-sea settings; Pemberton & Frey,

1985; Hubbard & Shultz, 2008). In deep marine settings, firmgrounds can commonly be formed on submarine canyon walls (Hayward, 1976). Pre-turbidite trace fossil assemblages show fidelity of preservation most closely comparable to that seen in firmground conditions. In deep-sea settings erosion of surface layers (presumably during sediment bypass) can also lead to the exhumation of stiff substrates at the sediment-water interface which may be subsequently colonized by benthic animals (Seilacher, 1964; Frey & Seilacher, 1980; Savrda, 1991; Savrda *et al.* 2001). Stiff sediments can allow the maintenance of an open burrow even when exposed to higher current activity and are easily identified in the rock record by well-defined burrow walls (Pemberton *et al.* 1992; Gingras *et al.* 1999). These firm burrow walls may preserve bioglyphs (i.e. scratch marks made by the animal(s) on the interior burrow wall; Frey *et al.* 1978, 1984). This is a common observation on *Thalassinoides suevicus* (*Spongeliomorpha*) burrows in dewatered shallow marine and deep marine substrates (Chapter 2; Frey *et al.* 1978; Schlirf, 2000). Organisms without appendages or setae have little potential to produce bioglyphs.

Grain-size is also an important consideration of the distribution of benthonic organisms, particularly in larval recruitment (Snelgrove *et al.* 1998, 2001). Grain-size has more relevance for adult mobile endobenthic organisms than for motile epibenthic or sessile endo- or epibenthic organisms as some animals are adapted to live in, manipulate, and deposit feed off material of a specific grain-size (Taylor *et al.* 2003). Some organisms are adapted to live in fine-grained sediment (e.g. the tracemakers of *Chondrites*, *Planolites*, and *Zoophycos*) whereas other organisms have a greater grain-size range (e.g. the progenitors of *Thalassinoides*, *Scolicia*, and *Phycosiphon*; Wetzel, 1984).

Grain-size is also a factor that plays a part in substrate repopulation and larval settlement with some benthos having species selectivity to grain-size (Ramey & Snelgrove, 2003). Planktonic larvae have been found to display grain selectivity when it comes to settling, choosing a grain-size range of their adult habitat (Snelgrove *et al.* 1998).

1.4. Deep-sea bioturbation: ichnofacies and ichnofabrics

Trace fossil distribution is dependent on the distribution of the tracemaking benthic community and the preservation potential of that community (Crimes, 1973). One of the first applications of ichnology was in placing ichnological assemblages into environmental distributions called ichnofacies. Ichnofacies are facies-controlled trace fossil assemblages that were considered to be temporally and spatially recurring through the Phanerozoic, controlled by the same set of palaeoenvironmental and depositional parameters (Seilacher, 1953a, 1953b). The original concept considered ichnofacies as bathymetrically-related groupings of trace fossils (Seilacher, 1964, 1967). Subsequent work has demonstrated that bathymetry is not the only first order parameter controlling the distribution of ichnofacies (Byers, 1982; Frey *et al.* 1990; Goldring, 1993, 1995). Current ichnofacies workers place greater importance on the full range of possible palaeoenvironmental controls rather than relying on ichnofacies as bathymetric indicators (Frey *et al.* 1990; Pemberton *et al.* 1992; MacEachern *et al.* 2007c). The four archetypal softground ichnofacies are described in Table 1.2 and their distribution is shown in Fig. 1.1.

Ichnofacies	Trace Fossil Features	Depositional Environment	Ichnogenera Present
Skolithos ichnofacies	Burrows are found to be vertically-orientated, cylindrical or U-shaped dwelling structures of suspension feeders. Trace fossil diversity is low with high abundances of ichnogenera possible.	The *Skolithos* ichnofacies is commonly found in moderate to high current energy settings in shifting sands. Such conditions are seen from the shoreface to tidal channels to proximal submarine fans.	Typical ichnogenera found in the *Skolithos* ichnofacies include *Arenicolites*, *Cylindrichnus*, *Diplocarterion*, *Gyrolithes*, *Macaronichnus*, *Ophiomorpha*, *Rosselia*, and *Skolithos*.
Cruziana ichnofacies	There is a mixture of vertical and horizontal traces in the *Cruziana* ichnofacies. There are trace fossils representing mobile epi- and endobenthos including carnivores, deposit feeders, and suspension feeders. Diversity and abundance of trace fossils is high.	It is found in muddy, shifting to stable substrates typical of shallow marine environments from fair weather wave base to depths above storm weather wave base.	Trace fossils found include *Asterosoma*, *Chondrites*, *Phycodes*, *Rhizocarallium*, *Rosselia*, *Taenidium*, *Thalassinoides*, and *Zoophycos*.
Zoophycos ichnofacies	The burrows in this ichnofacies are simple to complex feeding and grazing structures dominantly constructed by deposit feeders. There is a low diversity but high abundance of ichnogenera. There is a mix of shallow- and deep-penetrating burrows.	The *Zoophycos* ichnofacies is characteristic of low current energy, quiescent environments with low bottom waters and/or sediment pore water oxygenation found below storm wave base. The sediments are organic-rich muds or muddy sands.	Typical trace fossil ichnogenera include *Chondires*, *Helminthopsis*, *Phycosiphon*, *Planolites*, *Scolicia*, *Thalassinoides*, and *Zoophycos*.
Nereites ichnofacies	This ichnofacies is made of complex, shallow tier sediment grazers and farmers in the form of spiral burrows and nets and other complex shapes. These patterns represent an efficient deposit feeding strategy.	The *Nereites* ichnofacies was originally described by Seilacher for meandering and other surface trace fossils in deep-sea environments within and beyond the reach of turbidites to depths greater than 4000 m (Seilacher, 1964) designed to cope wit the low levels of nutrients in deep-sea settings (Seilacher, 1986). Diversity is high whereas abundances are low. The *Nereites* ichnofacies is found in bathyal and abyssal depths and intimately associates with inter-turbidite mudstone and hemipelagites and pelagites. The *Nereites* ichnofacies was considered to represent depths greater than 2000 m by Frey & Pemberton (1985).	Ichnotaxa found include *Helminthorhaphe*, *Lorenzinia*, *Megagrapton*, *Palaeodictyon*, *Spirophycus*, and *Zoophycos*.

Table 1.2. The four softground ichnofacies that characterized much of the marine sedimentary environment: description, general depositional environement, and characteristic trace fossils

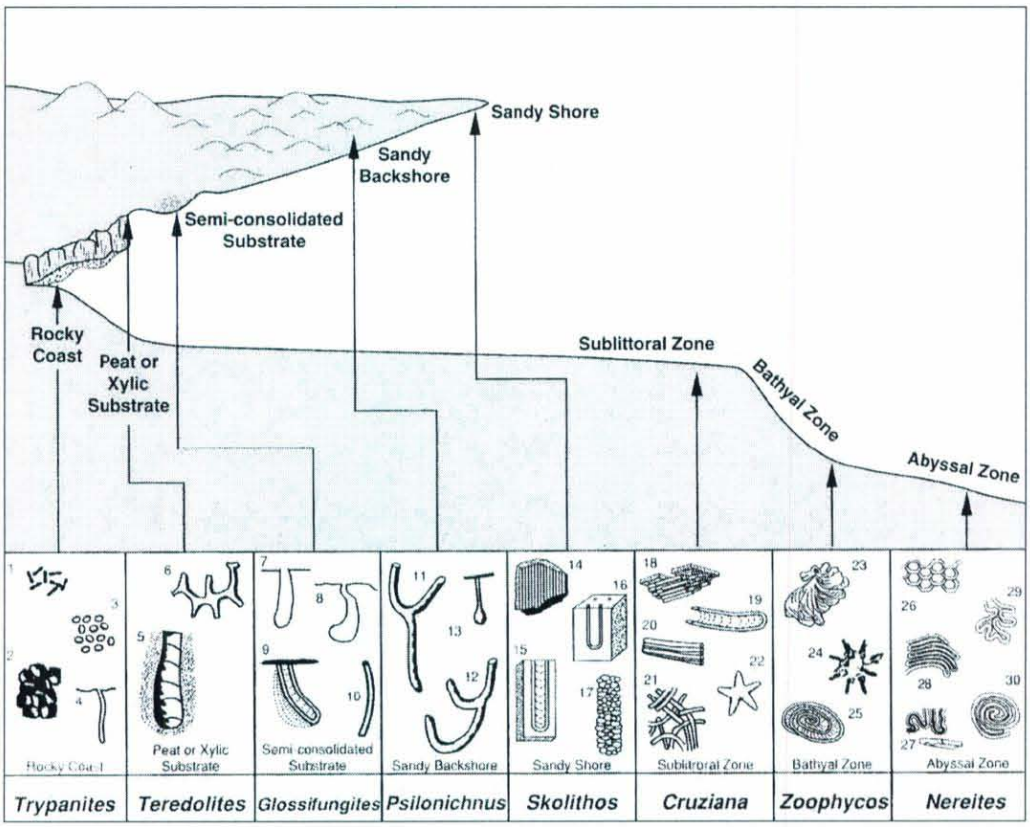


Fig. 1.1. The schematic bathymetric and environmental distribution of the four archetypal Seilachian softground ichnofacies (*Skolithos*, *Cruziana*, *Zoophycos*, and *Nereites;* see Seilacher 1953a, 1953b). Deep marine environments are categorized by the *Zoophycos* and *Nereites* ichnofacies. A description of each of the four softground ichnofacies is provided in Table 1.2. Other ichnofacies were introduced by subsequent authors to document trace fossil assemblages in other environments and substrates. Taken from MacEachern *et al.* (2007c).

1.4.1. Deep-sea ichnofacies

Approximately 70% of the planet's surface comprises a marine benthic habitat with the deep sea being arguably the largest ecosystem on the surface on the planet, covering approximately 40% of the Earth's surface (Quijón & Snelgrove, 2005). This vast area is dominated by two ichnofacies; the *Zoophycos* and *Nereites* ichnofacies (Seilacher, 1967) and three ichnosubfacies (the *Paleodictyon*, *Nereites*, and *Ophiomorpha rudis* ichnosubfacies of the *Nereites* ichnofacies; Seilacher, 1974, Uchman, 2001, 2009). The *Zoophycos* ichnofacies is a non-event, softground ichnofacies (i.e. it is not influenced by turbidity current or similar depositional processes; Seilacher, 2007). Trace fossils of the *Zoophycos* ichnofacies are characteristic of depositional environments ranging from offshore shelf to basin floor settings (Pemberton *et al.* 1992). The *Zoophycos* ichnofacies is mainly composed of deposit feeders living in quiescent environments with muddy substrates (Seilacher, 1967; Frey & Seilacher, 1980; Seilacher, 2007). The eponymous trace fossil *Zoophycos* has been found in various palaeoenvironments through the Phanerozoic. During the Palaeozoic it was found in both nearshore and slope environments but left the nearshore in the Mesozoic and retreated off the continental shelf in the Cenozoic (Bottjer *et al.* 1988; Kotake, 1991; Knaust, 2004). In the modern ocean, *Zoophycos* is found in deep-sea settings below 2000 m water depth (Wetzel & Werner, 1981; Wetzel, 1983, 1984, 2008). The onshore-offshore migration could be the result of fine-grained mud substrates being deposited in nearshore environments during the Palaeozoic (Bottjer *et al.* 1988). Components of the *Zoophycos* ichnofacies, including *Zoophycos* itself, are conventionally interpreted as opportunistic tracemakers including

surface grazers and endobenthic deposit feeders in low oxygen and low energy environments (Frey & Seilacher, 1980; Kotake, 1989, 1991; MacEachern *et al.* 2007c). An alternative interpretation of the ethology of *Zoophycos* suggests that the trace-making organism was farming microbes in the burrow walls (Bromley, 1991; Fu & Werner, 1995; Bromley & Hanken, 2003). Microbial farming is perhaps a more common method of feeding in the marine realm than previously thought (see Chapter 3).

The *Nereites* ichnofacies is a softground ichnofacies characterized by deposition of material from the photic zone that is episodically interrupted by deposition from turbidity currents (Wetzel, 2002; Seilacher, 2007). The relatively long-term stability of the deep ocean floor has led to a high degree of specialization in benthic forms. High diversities of burrowing activities and trace fossil assemblages are documented in deep-sea and abyssal settings with the maintenance of an equilibrium community of K-strategists (Sanders, 1968; Ekdale, 1980, 1985). Deep marine trace fossil assemblages can also be characterized by delicate, geometrical traces (graphoglyptids; Seilacher, 1977) forming complex near-surface burrows to exploit the nutrient-deficient, but oxygenated, sediment and bottom waters in deep-sea settings (Ekdale, 1980; Frey & Seilacher, 1980; Wetzel, 2002). The *Nereites* ichnofacies is found from lower bathyal to abyssal depths (MacEachern *et al.* 2007c) with modern occurrences below 4000 m water depth (Wetzel, 2002). Preservation of the *Nereites* ichnofacies requires turbidity currents of weak erosive power to expose the burrows and cast them with sediment transported by the waning currents (Seilacher, 1977; Wetzel, 1984; Orr, 1995). Recently it has been suggested that preservation of pre-depositional assemblages is due to a shock wave ahead of the turbidity current which sucks unconsolidated material into suspension without

significant erosion of delicate burrows which are then sand cast (Seilacher, 2007). The *Nereites* and *Zoophycos* ichnofacies describe large areas of continental slope and basin plain if conditions are unchanging and stable over periods of time. As a result, ichnosubfacies were introduced to document the trace fossil components within these environments (Seilacher, 1974, Uchman, 2001, 2009). For example, the *Paleodictyon* and *Nereites* ichnosubfacies of the *Nereites* ichnofacies were erected to describe assemblages found in sandier and muddier substrates of deep, distal turbidites, respectively (Seilacher, 1974). The *Ophiomorpha rudis* ichnosubfacies of the *Nereites* ichnofacies was introduced by Uchman (2001) to describe the high abundances of *Ophiomorpha rudis* found in the thick-bedded sandstone turbidites associated with channels and proximal lobe settings (discussed in detail by Uchman, 2009 and documented in Chapter 2 & 3 in terms of ichnofabric).

1.4.2. Deep-sea ichnofabrics

Another method of describing and interpreting the ichnology of ancient and modern sediments is *ichnofabric analysis* (Bockelie, 1991; Knaust, 1998; McIlroy, 2004a). Ichnofabric analysis is a tool which has successfully been used to document and describe a variety of, mostly shallow marine, palaeoenvironments (Martin & Pollard, 1996; McIlroy 2004b; Garton & McIlroy, 2006; Gibert & Goldring, 2007). An *ichnofabric* description documents the texture and internal structure of a rock or sediment as result of bioturbation and bioerosion at all scales (Ekdale & Bromley, 1983). Ichnofabric analysis can be carried out simultaneously with facies analysis so both sets of data can be directly

compared and correlated (McIlroy, 2008). This detailed bed-by-bed approach lends itself to the subtleties encountered in the rock record and makes for a comprehensive study of any field outcrop or cored stratigraphic succession (Goldring, 1995, Taylor *et al.* 2003; McIlroy, 2004a, 2004b, 2007).

Combining ichnological data with analysis of physical sedimentary structures is widely used to improve palaeoenvironmental analysis (Chapters 2 & 4; Taylor & Goldring, 1993; McIlroy, 2004a, 2004b, 2008). The ichnofacies concept has been found to be too broad and generalized for some study areas (Martin & Pollard, 1996). There has also been migration of ichnogenera on- and offshore through the Phanerozoic, *Zoophycos* being an example (Bottjer *et al.* 1988). These temporal changes in the distribution of ichnotaxa into different environments weakens the ichnofacies concept as the palaeoenvironmental setting of deep marine trace fossils has not been uniform through the Phanerozoic. The ichnofacies method has been criticized for not having sufficient resolution to detail to account for bed-by-bed changes in ichnodiversity and ichnometry (Goldring, 1993; McIlroy, 2004a). The ichnofabric method is favoured and developed in this thesis.

1.5. Contributions to the ichnology and ichnofabrics of deep marine systems

1.5.1. Turbidite ichnofabrics

Turbidite successions preserve two contrasting sets of seafloor conditions. Pre-turbidite conditions are characterized by hemipelagic or pelagic sedimentation (Leszczyński, 1991). Periods of active turbidity current deposition are characterized by an increase in current energy, sedimentation rate, and often by a change in lithology (Wetzel, 1984). Turbidite deposition changes the sedimentological and geochemical conditions on the seafloor (Wilson *et al.* 1985; Thomson *et al.* 1987; Burton & Link, 1991; Orr, 1994; Meyers *et al.* 1996; Mángano & Buatois, 1997; Wetzel & Uchman, 2001; Uchman, 2004) and subsequently influences the composition and ethology of the benthic community (Chapter 2; Heard & Pickering, 2008). These changes in the benthic environment lead to the juxtaposition of different ichnocoenoses indicative of the different environments (Bromley & Ekdale, 1986).

Turbidite successions contain pre- and post-depositional trace fossil assemblages (Seilacher, 1962; Kern, 1980; Orr 1994; Heard & Pickering, 2008; Buatois *et al.* 2009). Pre-depositional assemblages represent time-averaged, deep-sea ecosystems prior to event bed deposition. Numerous tracemaker ethologies can be preserved in pre-event strata including grazing, farming, and near-surface deposit feeding (Uchman, 1995, 1998). Preservation of pre-depositional assemblages commonly occurs as a result of sand-casting by turbidity currents of low erosive power (Seilacher, 1977; Leszczyński, 1991). Trace fossil diversity in these assemblages is generally high and include many

from the graphoglyptid group (Frey & Seilacher, 1977, 1980; Uchman, 1995, 1998; Bromley, 1996). Inter-turbidite conditions are temporally dominant even though sand can dominate the outcrop in turbidite successions (Kern, 1980). Pre-event assemblages are made by K-selective organisms which developed niche specialization between turbidity current events (Sanders, 1968; Ekdale, 1985; Gage, 1996). Inter-turbidite and pelagic sediments have lower accumulation rates than nearshore and shelf environments, and are dominated by productivity-derived material (Ekdale & Bromley, 1984). As a result pre-depositional and pelagic assemblages can remove all primary sedimentary structures producing a burrow homogenized fabric and complex overprinting of trace fossils (Chapters 2 & 4; Doeven, 1983; Bromley & Ekdale, 1984; Wetzel, 2002; Macquaker & Adams, 2003).

Post-depositional assemblages are composed of opportunistic r-strategists (Ekdale, 1985) characterized by lower ichnodiversity and higher abundances of deep-burrowing ichnogenera like *Ophiomorpha* and *Thalassinoides* (Chapter 2; Uchman, 2009). Turbidity currents can have high sedimentation rates relative to pelagic/hemipelagic accumulation (e.g. a turbidite 27 cm thick can be deposited in tens of minutes; Allen, 1991). As a result deep-burrowing organisms have a competitive advantage in the aftermath of turbidity currents, able to exploit the resources in buried hemipelagite (Chapters 2 & 3).

Within a turbidite system there are commonly ichnological differences between sub-environments (Crimes, 1973; Crimes & Fendonkin, 1994; Uchman, 2001; Heard & Pickering, 2008). The component architectural elements of a turbidite system may display a range of environmental conditions so the benthic organisms in those areas show

different tracemaker ethologies. An example of this facies-associated ichnological variability within a turbidite system is illustrated in Chapter 2. In Chapter 2 the ichnology and ichnofabrics of an ancient turbidite setting are examined. The Grès d'Annot Basin, SE France, has excellent exposure making logging continuous sections of many depositional environments possible. The basin is well-studied with a well-developed sedimentology and stratigraphy framework in place (Apps *et al.* 2004; Callec, 2004). The Grès d'Annot Basin is a thrust sheet-top basin made of several sub-basins bound by structural highs (Apps *et al.* 2004). The Eocene/Oligocene Grès d'Annot Formation is a sand-rich, coarse-grained turbidite succession deposited into the confined Grès d'Annot Basin. The confining topography in the basin led to the formation of many depositional sub-environments including bounding slopes, channel areas, and depositional lobes on the basin floor.

Chapter 2 looks at the variety of depositional environments within a confined turbidite system and analyses them from an ichnological standpoint. The following questions are proposed: How do ichnology and ichnofabric change from one part of the turbidite system to another? What are the changes within each sub-environment over time (i.e. how does tracemaker ethology change with increases or decreases in current energy in turbidite systems)? Are there any changes in pre- and post-depositional assemblages in the Grès d'Annot Formation? From all these data, can trace fossils and ichnofabrics be used as good indicators of deep-marine depositional environments? There have been several papers on the ichnofabrics of deep-water pelagic carbonate sediments (Bromley & Ekdale, 1983, 1984; Locklair & Savrda, 1989a, 1989b) but very few deep-water ichnofabric studies have been made on deep-water siliciclastic sediments,

turbidite systems in particular (Knaust, 1998, 2009). This thesis is a step forward to the contribution of ichnofabrics to better understand the response of deep-sea benthos to changes in the depositional environment in turbidite settings.

1.5.2. Sandstone-mudstone interface trace fossils: a common feeding strategy in marine systems

Inter-turbidite sediments may include organic matter transported from source areas on the continental shelf or slope (Wilson *et al.* 1985). Burial of fine-grained sediment below turbidite sandstone increases the preservation potential of organic carbon as it is buried in a geochemically closed system beyond the reach of all but deepest burrowers (Macquaker & Gawthorpe, 1993; Meyers *et al.* 1996). This buried resource can be exploited by deep-burrowing, post-depositional tracemakers (Chapters 2 & 3; Miller, 1984; Uchman, 2001, 2009).

Ophiomorpha and *Thalassinoides* are two deep-burrowing ichnogenera which are found in many post-depositional assemblages (Chapter 2; Wetzel, 1991b; Uchman, 2007, 2009; Heard & Pickering, 2008). Post-depositional *Ophiomorpha* exceed 2 m in length (from the top to sole of sandstone turbidites) in the Grès d'Annot Formation before ramifying at depth in inter-turbidite mudstone or along a sandstone-mudstone interface (Chapter 2; Uchman, 2007). This distribution of *Ophiomorpha* and *Thalassinoides* was seen throughout the Grès d'Annot Formation and has been observed from other turbidite basins worldwide (Chapter 2; Uchman, 1995, 1998, 2001, 2009; Heard & Pickering, 2008). This paper asks why the *Ophiomorpha/Thalassinoides* animal should burrow

through thick-bedded turbidites to sand-mud interfaces and exploit them so fully leading to the high trace fossil density found on sandstone turbidite tops and soles.

In order to address this question, mesocosm experiments were established with modern analogues of the *Ophiomorpha* and *Thalassinoides* tracemakers. The tracemaker chosen for this experiment was the thalassinid ghost shrimp *Neotrypaea californiensis* acquired from the mud flats of Oregon, USA (by Ted DeWitt, Environmental Protection Agency). Thalassinid shrimp are well-documented progenitors of *Ophiomorpha* and *Thalassinoides* found in a variety of shallow water and intertidal settings (Chapter 3; Weimer & Hoyt, 1964; Frey *et al.* 1974; Uchman, 1995; Miller & Curran, 2001). Shallow marine examples were chosen due to the difficulty in obtaining deep-marine shrimp. Analogue experiments were constructed to simulate turbiditic stratification (details in Chapter 3). Introduced tracemakers are hypothesised to burrow to sand-mud interfaces and then along the lithological boundary producing interface burrows analogous to ancient examples (see examples in Chapter 2).

It has long been postulated that microbes in fine-grained inter-turbidite sediment might provide a source of nutrition for burrowing organisms rather than the fine-grained material itself (MacGinitie 1978; Miller, 1984; Uchman, 2009). This, until now, has remained untested. It is here hypothesised that *Neotrypaea californiensis* will burrow down to, and along, sand-mud interfaces in our mesocosms to exploit and farm microbial populations between muddy sediments (containing organic carbon) and comparatively well-oxygenated, and organic carbon-limited sand (relative to the background muddy sediment). Bioirrigation of deep burrows allows deep-sediment oxygenation and maintenance of aerobic microbial populations within the burrow walls which the

tracemaker can utilize as a nutritional resource. This hypothesis will be tested in this paper. Burrow distributions will be mapped in three dimensions using CT imagery and samples taken from the mesocosms for TOC and stable isotope analysis to determine whether *N. californiensis* is changing the sediment geochemistry to meet its nutritional requirements.

These experiments aim to record the range of behaviours exhibited by modern trace-making organisms and their response to differing sediment profiles. The mesocosm experiments conducted herein aim to provide an explanation for why ancient deep-burrowing organisms, such as the *Ophiomorpha*-progenitors, preferentially exploit sandstone-mudstone interfaces in turbidite systems. The incentive for such deep burrowing behaviour has hitherto been obscure.

1.5.3. Ichnofabrics associated with pelagic sedimentation

Deep ocean floors, away from the influence of turbidity currents, are entirely subject to pelagic deposition (Gooday & Turley, 1990). Pelagic or hemipelagic steady-state conditions are typified by low sediment accumulation rates (Doeven, 1983; Bromley & Ekdale, 1984; Wetzel, 2002). The material that reaches the ocean floor is almost entirely sourced from the photic zone and comprises of planktonic debris, and faecal pellets flocculated into 'marine snow' (Gooday & Turley, 1990). Above the calcite compensation depth (CCD) sediment is dominantly productivity derived (i.e. nannoplankton-rich) with little or no clastic dilution by allochthonous components (Macquaker & Gawthorpe, 1993; Macquaker & Adams, 2003). Detrital material

delivered to the deep seafloor is commonly wind-blown silt-grade material (loess; Wetzel, 1984). Deep-water and abyssal environments are oxygenated, but commonly nutrient-deficient (Jumars *et al.* 1990) resulting in a tiered endobenthic community in the substrate, maximizing available resources (Ausich & Bottjer, 1982). Infaunal tiering is well-defined and well-documented as organisms reside at different depths in the sediment related to species specific preferences for substrate firmness, oxygenation, and differences in feeding behaviour (Berger & Heath, 1968, Wetzel, 1981, 1983, 1991b; Ekdale *et al.* 1984; Bromley & Ekdale, 1986; Savrda & Bottjer, 1989b).

Endofaunal tiering in sediments has a tripartite stratigraphy including an upper *mixed layer*, an intermediate *transition layer*, and a lower *historical layer* (Fig. 1.2; Berger *et al.* 1979; Wetzel, 1984, 1991b). The mixed layer is a layer of water-saturated sediment, burrow-homogenized by meiofauna extending from the sediment-water interface 3-15 cm into the substrate (Berger *et al.* 1979; Ekdale *et al.* 1984; Savrda & Bottjer, 1989a; Bromley, 1996). Continual bioturbation reduces the shear strength of the mixed layer making it easily remobilized by bottom currents (Savrda & Bottjer, 1989a). The mixed layer has been observed in box cores taken from Recent deep-sea sediments (Berger *et al.* 1979; Ekdale *et al.* 1984; Werner & Wetzel, 1981; Wetzel, 2008). Below the mixed layer is the transition layer, composed of dwelling and feeding structures of deeper burrowing organisms (Savrda & Bottjer, 1989a). Active burrowing leads to heterogeneous mixing of the sediment in the transition layer (Ekdale *et al.* 1984). The thickness of the transition layer was found to be 20-35 cm thick in the eastern equatorial Pacific by Berger *et al.* (1979). The historical layer defines the depths in the sediment below the reach of bioturbating organisms and is characterized by a burrow-homogenized

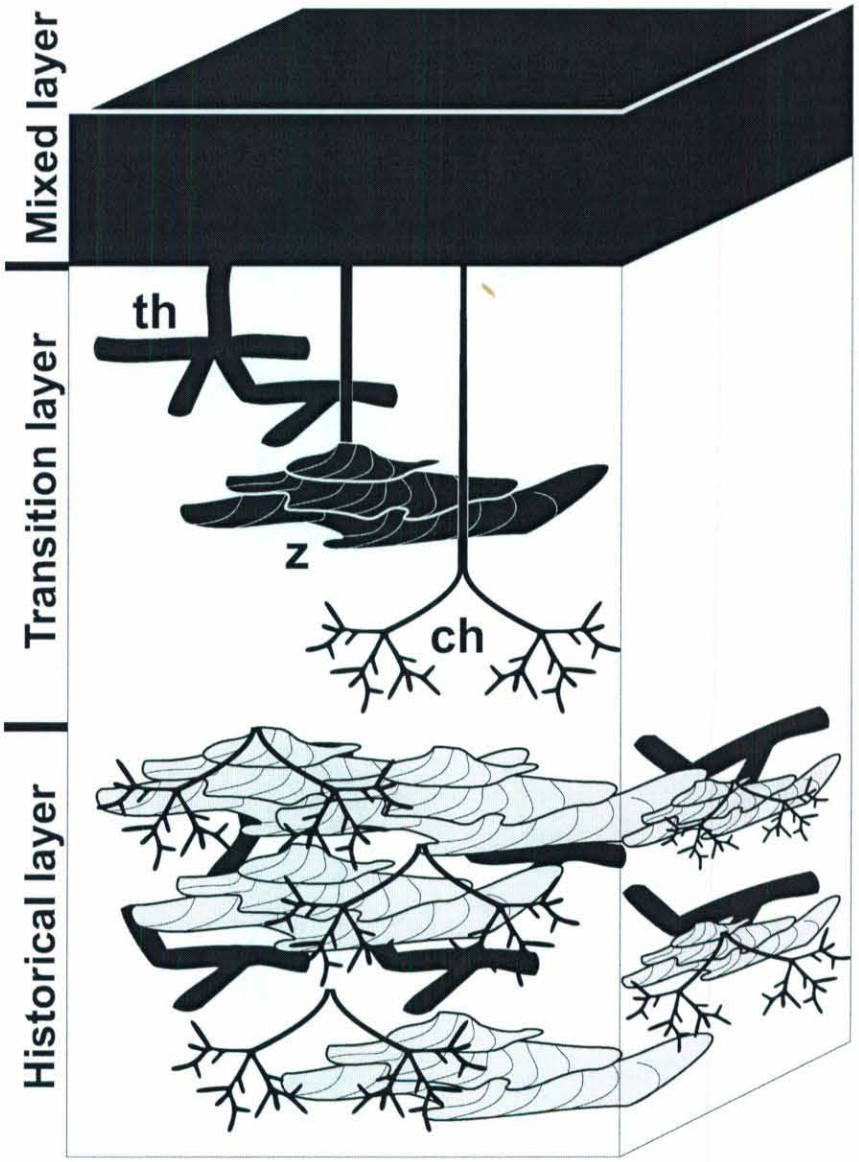


Fig. 1.2. Schematic diagram showing the generalized stratigraphy and archetypical tiering of trace fossils as can be found under steady state pelagic conditions. Three ichnogenera are used to illustrate the effect of continual overprinting under low sediment accumulation rates. *Thalassinoides* (th) is commonly overprinted by *Zoophycos* (z). Both ichnogenera are overprinted by the deep-tier trace fossil *Chondrites* (ch).

ichnofabric (when bioturbation is complete), overprinted by trace fossils from the transition layer (Locklair & Savrda, 1998a, 1998b). The historical layer characterizes most deep-water mudstone facies, siliciclastic mudstones, marls and chalks (Chapter 4; Ekdale & Bromley, 1983, 1984).

Chapter 2 documents the trace fossil assemblages and ichnofabrics of pelagic sediments (an end-member system). The outcrops at Montagne de Chalufy, Grès d'Annot Basin, SE France, (Chapter 2) document vagile, near-surface deposit feeders and farmers utilizing organic carbon in fine-grained sediment between turbidity current episodes. Likewise, Chapter 4 describes the autochthonous Wyandot Formation, offshore Nova Scotia, which preserves similar tracemaker ethologies, related to low sediment accumulation rates. The Wyandot Formation is intensely bioturbated reservoir facies with the loss of all primary sedimentary fabric (Ings *et al.* 2005). When intense bioturbation destroys all the primary sedimentary fabric, ichnofabrics and trace fossil assemblages can be used to decipher palaeoenvironmental conditions (Bottjer & Savrda, 1986, 1989a, 1998b; Savrda, 1991, 1995; Wetzel, 1991b). The Wyandot Formation is used as a case study to assess the usefulness of trace fossil analysis and the ichnofabric method in reconstructing depositional environments and identifying stressed conditions in the rock record of pelagic systems. This paper also investigates the textual and mineralogical impact of bioturbating organisms and its effect on reservoir quality. Deposit feeding endofauna have the potential to introduce heterogeneity into the sediment by biodeposition (of faecal pellets). Studies on the effect of bioturbation of reservoir properties have mainly focussed on siliciclastic systems (Gingras *et al.* 2007; Tonkin *et al.* 2010). Chapter 4 includes a petrographic study of the Wyandot Formation to examine

whether the burrowing organisms have had any effect on the mineralogy of the sediment, and if so, could it influence reservoir quality of carbonate systems?

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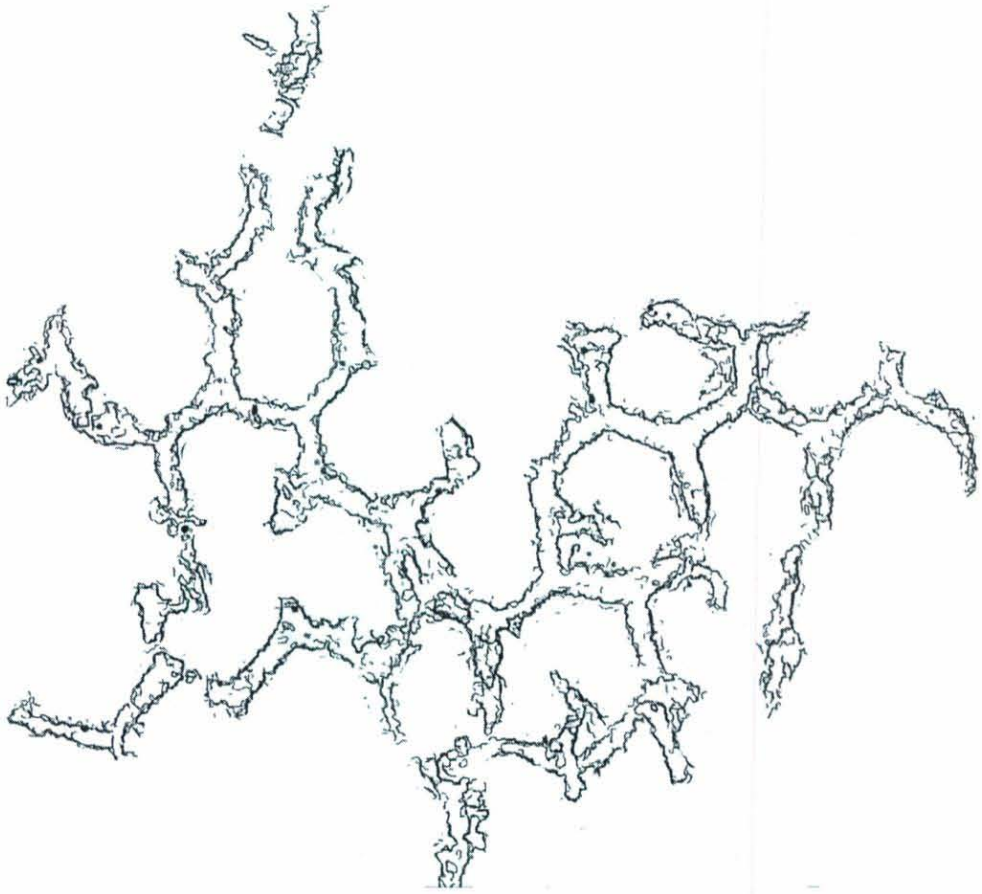
CHAPTER 2

Ichnological characterization of Eocene/Oligocene turbidites from the Grès d'Annot Basin, French Alps, SE France



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CHAPTER 2

Ichnological characterization of Eocene/Oligocene turbidites from the Grès d'Annot Basin, French Alps, SE France

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Abstract

The ichnology of the Grès d'Annot Basin, SE France, is described in detail for the first time. Deep marine palaeoenvironments from basin slope to basin floor settings are preserved. The Grès d'Annot Formation is a sand-rich, thick-bedded, and coarse-grained turbidite succession. The Marnes Brunes Inférieures Formation is a succession of thin-bedded, fine-grained turbidites interpreted as lateral and distal equivalents of the Grès d'Annot Formation. The siliciclastic basin fill is highly bioturbated and characterized by low diversity, high abundance ichnological assemblages which are described herein. Trace fossil and ichnofabric analysis of the Grès d'Annot Basin are used as tools for interpreting palaeoenvironmental and depositional changes.

Heterolithic successions of thin-bedded turbidite sandstone and inter-turbidite mudstone contain the most diverse trace fossil assemblages found in the Grès d'Annot

Basin. Sedimentological and ichnological data suggests that heterolithic facies are found on either relatively quiescent confining slopes either as lateral or distal equivalents of larger turbidites or as channel-fill deposits. In these settings trace fossil assemblages are dominated by the deposit feeding activity of vagile, endobenthic organisms (e.g. *Ophiomorpha*, *Phycosiphon*, *Planolites*, and *Scolicia*).

Thick-bedded and channel sandstones contain low diversity trace fossil assemblages dominated by *Ophiomorpha*. *Ophiomorpha* in the Grès d'Annot Basin is inferred to have been produced by organisms mostly deposit feeding on buried organic-rich material during inter-turbidite intervals. *Ophiomorpha rudis* is the most prominent trace fossil found in the Grès d'Annot Basin and dominates the ichnofabrics in all locations within the basin. The deep-burrowing ability of the *Ophiomorpha* animal is considered to be an adaptation for exploiting buried organic nutrients found in inter-turbidite mudstones.

2.1. Introduction

The deep marine, currently comprising approximately 40% of the Earth's surface, is perhaps the single most widespread depositional environment. This vast ecosystem has been greatly understudied with respect to palaeo- and neoichnology in comparison with shallow-marine settings. This disparity is partly due to the technological challenges of studying modern deep marine settings. This work details trace fossil assemblages of the Grès d'Annot Basin, one of the best preserved, and well exposed, ancient deep-water

systems (Sinclair, 1997; Kneller & McCaffrey, 1999; 2003; Apps *et al.* 2004). Large-scale facies architecture and its relationship to process sedimentology and basin structure have been well constrained, but no study has focused specifically on the ichnology of the Grès d'Annot Formation. The pre-existing sedimentological and stratigraphic framework makes this an ideal site for an integrated ichnological and sedimentological analysis of an ancient, deep-water depositional system.

Bioturbation and bioerosion, and the ichnofabrics they produce in sediments have many applications particularly for palaeoenvironmental and stratigraphic studies (Taylor *et al.* 2003; McIlroy, 2004a, 2008). Trace fossils preserve the response of benthic organisms to prevailing environmental and depositional conditions. To this end, they are constructive to workers in many different disciplines as they provide data that can aid in: (1) the identification of key stratal surfaces, usually omission surfaces (MacEachern *et al.* 1991; 2007a; Ghibaudo *et al.* 1996); (2) the identification of stressed conditions on the seafloor (Uchman, 2004; MacEachern *et al.* 2007b); and (3) interpreting palaeoenvironments both in outcrop and in core (Pemberton *et al.* 2001; McIlroy, 2004a, 2004b, 2007, 2008; MacEachern *et al.* 2007c). The application of these approaches to the study of deep marine and turbidite depositional systems are being developed.

This paper uses the Grès d'Annot turbidite system to develop trace fossils and ichnofabrics as depositional and environmental indicators in deep-sea siliciclastic turbidite systems. It is the first detailed account of the ichnological assemblages of the Grès d'Annot Formation and Basin. The paper uses trace fossil assemblages as tools for highlighting changes in the palaeoenvironmental and depositional conditions during the deposition of the siliciclastic basin fill.

2.2. Methodology

Excellent exposure within the Grès d'Annot Basin allows detailed logging of extensive areas and sections of cliff-face. The main focus of this work was to document the trace fossils in the sand-rich Grès d'Annot Formation which had hitherto had not been documented in detail. In areas of onlap with the Grès d'Annot Formation the trace fossils of the underlying Marnes Brunes Inférieures Formation and Marnes Bleues Formation were also studied. This paper centres on work carried out in four areas (Fig. 2.1). Facies architectural elements logged include channel sands and channel-fill at the Col de la Cayolle area, a proximal fan environment at Baisse de l'Aiguille, and basin slope settings (onlap surfaces) at the Braux and Montage de Chalufy outcrops (Fig. 2.1).

2.3. Geological Setting

The Grès d'Annot Basin is not a foreland basin *sensu stricto*, but a thrust sheet-top (piggyback) basin formed behind the thrust front on top of already compressed and shortened crust (Apps *et al.* 2004). As a result, the Grès d'Annot Basin and other thrust sheet-top basins are found localized in the synclinal sectors of compressional structures and are topographically complex (Apps *et al.* 2004; Ford & Lickorish, 2004).

The fill of the Grès d'Annot Basin shows a sharp deepening following basin formation, to its eventual filling (Fig. 2.2). The Calcaires Nummulitiques Formation is a regionally extensive shallow marine bioclastic limestone unit consisting of patch reefs

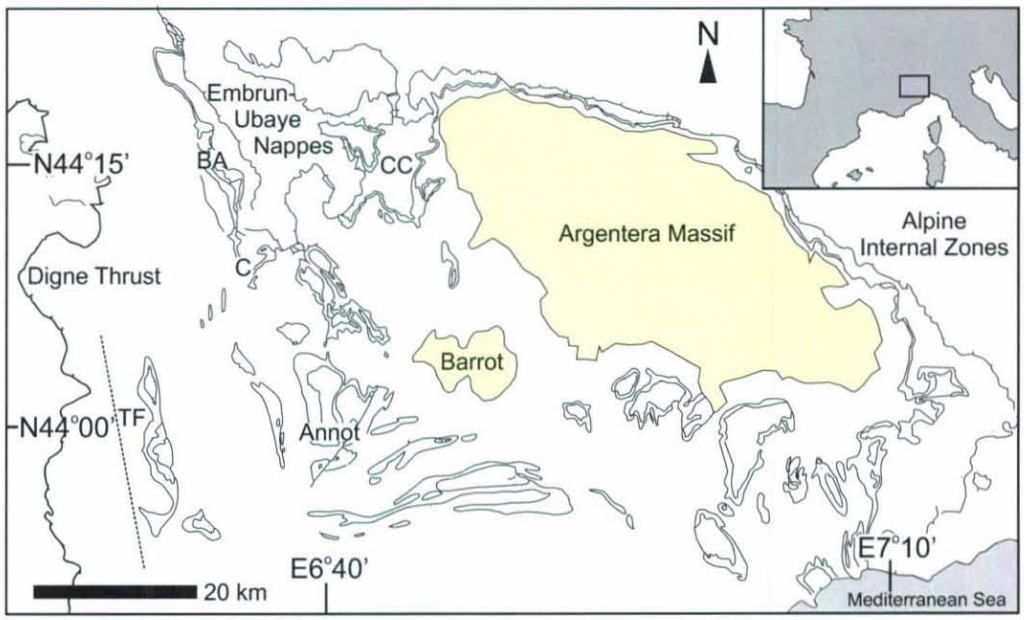


Fig. 2.1. A map of the study area. Tertiary outliers (Marnes Brunes Inférieures and Grès d'Annot Formations; unfilled outlines) and pre-Mesozoic inliers (labelled and filled yellow). The dashed line marked TF indicates the position of the initial (Eocene) thrust front that established the province of thrust sheet-top basins to the east. Locations referred to in the text are labelled: BA, Baisse de l'Aiguille; C, Montagne de Chalufy; CC, Col de la Cayolle. The outcrops studied at Argenton and Braux are located close to the town of Annot. Image modified from Apps *et al.* (2004).

made by accumulations of giant nummulite foraminifers (Apps *et al.* 2004). Its deposition represents transgression of the basin margin during a period of relative sealevel rise induced by flexural loading of the crust by the Alpine Orogeny (Callec, 2004). The overlying Marnes Bleues Formation is a deep-water, mudstone-dominated succession deposited during a phase of rapid subsidence and low sediment supply. Basin deepening is evident from a gradual loss of shallow-water benthic foraminifera to the dominance of planktonic species at higher stratigraphic levels. Water depths of approximately 900 m are estimated from the uppermost marls in this formation (Apps *et al.* 2004). The last phase of basin fill is dominated by deep-water sands and mass wastage deposits of the advancing Alpine Orogeny (Sinclair, 1997). These siliciclastic deposits consist of thin-bedded turbidites of the Eocene Marnes Brunes Inférieures Formation which are interpreted as the lateral and distal equivalents of the thick-bedded turbidites of the 500 to 1,500 m thick Eocene/Oligocene Grès d'Annot Formation (Stanbrook & Clark, 2004).

At the time of turbidite deposition regional tectonics had folded and continued to fold the underlying strata producing a province of thrust sheet-top basins in which structural highs bound confined sub-basins (Apps *et al.* 2004). Turbidite deposition suppressed the basin floor topography onlapping it and eventually filling the basin (Sinclair, 2000). The provenance of these turbidites could have been a southerly granitic source, the Corsica-Sardinia and Maurès-Esterel Massifs (Apps *et al.* 2004) or a source to the east, possibly early Alpine, or a NE extension of the Corsica-Sardinia Massif.(now removed by erosion; Apps, 1987).

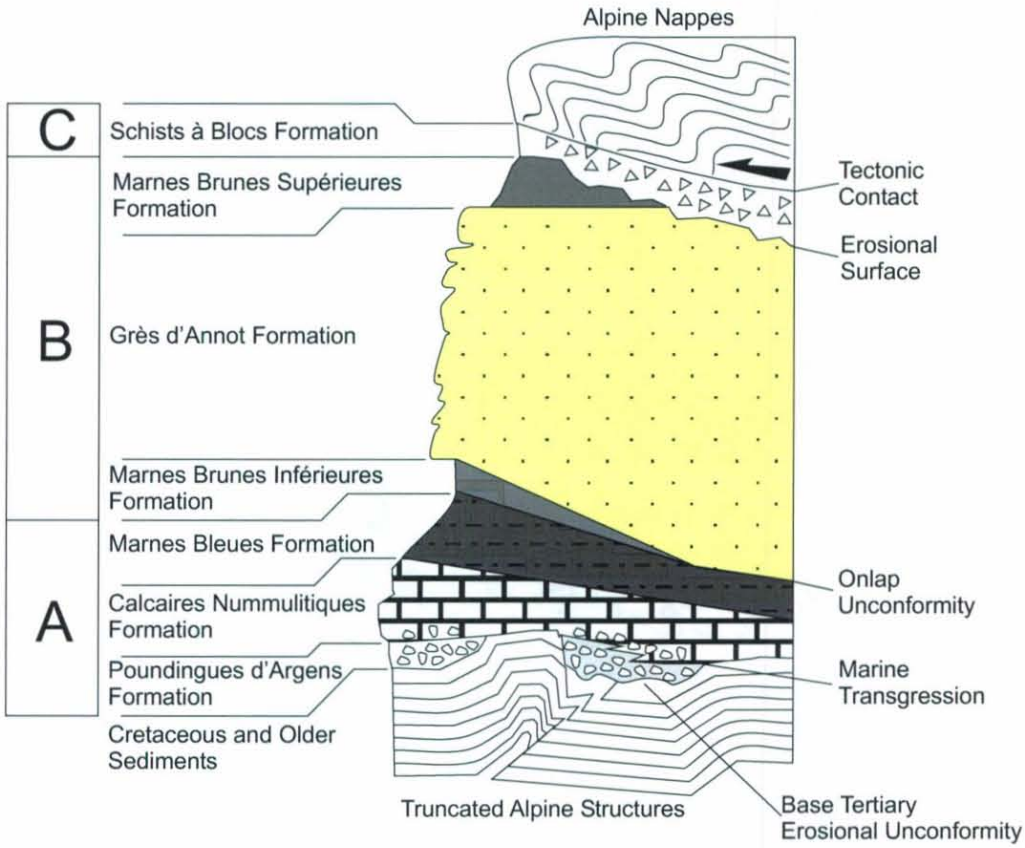


Fig. 2.2. A stratigraphic column of the Cenozoic sedimentary fill of the Grès d'Annot Basin divided into related units. **A.** Genetic units from the initiation and deepening of the basin (Calcaires Nummulitiques and Marnes Bleues Formations). **B.** Genetic units from the basin filling stage (Marnes Brunes Infèrieures and Grès d'Annot Formations). **C.** Genetic units representing the closure of the basin (Schists á Blocs Formation). Diagram not drawn to scale. Modified from Apps *et al.* (2004).

Eocene-Miocene rifting of eastern Iberia diverted sediment supply away from the Grès d'Annot Basin (Séranne, 1999; Brunet *et al.* 2000). The remaining accommodation space was filled by the overlying Schists à Blocs Formation which is composed of debris shed from the Embrun-Ubaye Nappes (Apps *et al.* 2004). These factors, in combination, caused turbidite deposition to cease in the Late Rupelian.

2.4. Systematic ichnology

Although ichnodiversity does not directly correspond to biological diversity, it has conventionally been used as a proxy for the benthic behavioural diversity on the palaeo-seafloor (McIlroy, 2004a; Herringshaw *et al.* 2010). Low ichnological diversity is thought to indicate physiologically stressful seafloor conditions including salinity stress, low bottom water oxygenation, and nutrient stress (MacEachern *et al.* 2007b). Higher ichnological diversity can infer palaeoenvironmental conditions more hospitable to benthic life. Previous studies of the Grès d'Annot Basin have been sedimentological and have not focused on the ichnodiversity of the various facies architectural elements. In doing so, they have neglected a significant source of palaeoenvironmental information that could be used to constrain depositional conditions. The Marnes Bleues Formation was discovered to have a sparse and restricted ichnofauna. The turbidites of the Marnes Brunes Inférieures Formation and the Grès d'Annot Formation have an abundance of trace fossils, though trace fossil assemblages are of low diversity. The distribution of trace fossils in the studied units of the Grès d'Annot Basin is patchy (Table 2.1). This

Ichnogenera	Sand-dominated facies				Heterolithic facies		Mud-dominated facies	
	Facies 1	Facies 2	Facies 3	Facies 4	Facies 5	Facies 6	Facies 7	Facies 8
?Asterosoma radiciforme						R		
Chondrites isp.		C			R			
Diopatrichnus isp.								R
Ophiomorpha annulata		C			C	C		
Ophiomorpha ?nodosa			R					
Ophiomorpha rudis	C	C	R		C	C	C	
Paleodictyon majus		R			C			
Phycodes isp.		R						
Phycosiphon isp.						R		
Planolites isp.		C			C	R		
Scolicia prisca						R		
Thalassinoides suevicus	C	C			R		R	
Zoophycos isp.					R			

Table 2.1. The distribution of ichnotaxa recorded within the described facies of the Grès d'Annot Basin. Trace fossils that are rare in a facies are identified with R. Ichnogenera that are common in a facies are identified with C.

small-scale patchiness is characteristic of other studied deep-water sandstone successions (Uchman, 1995a, 1999, 2001). A systematic description of the ichnotaxa found within the studied areas is presented below.

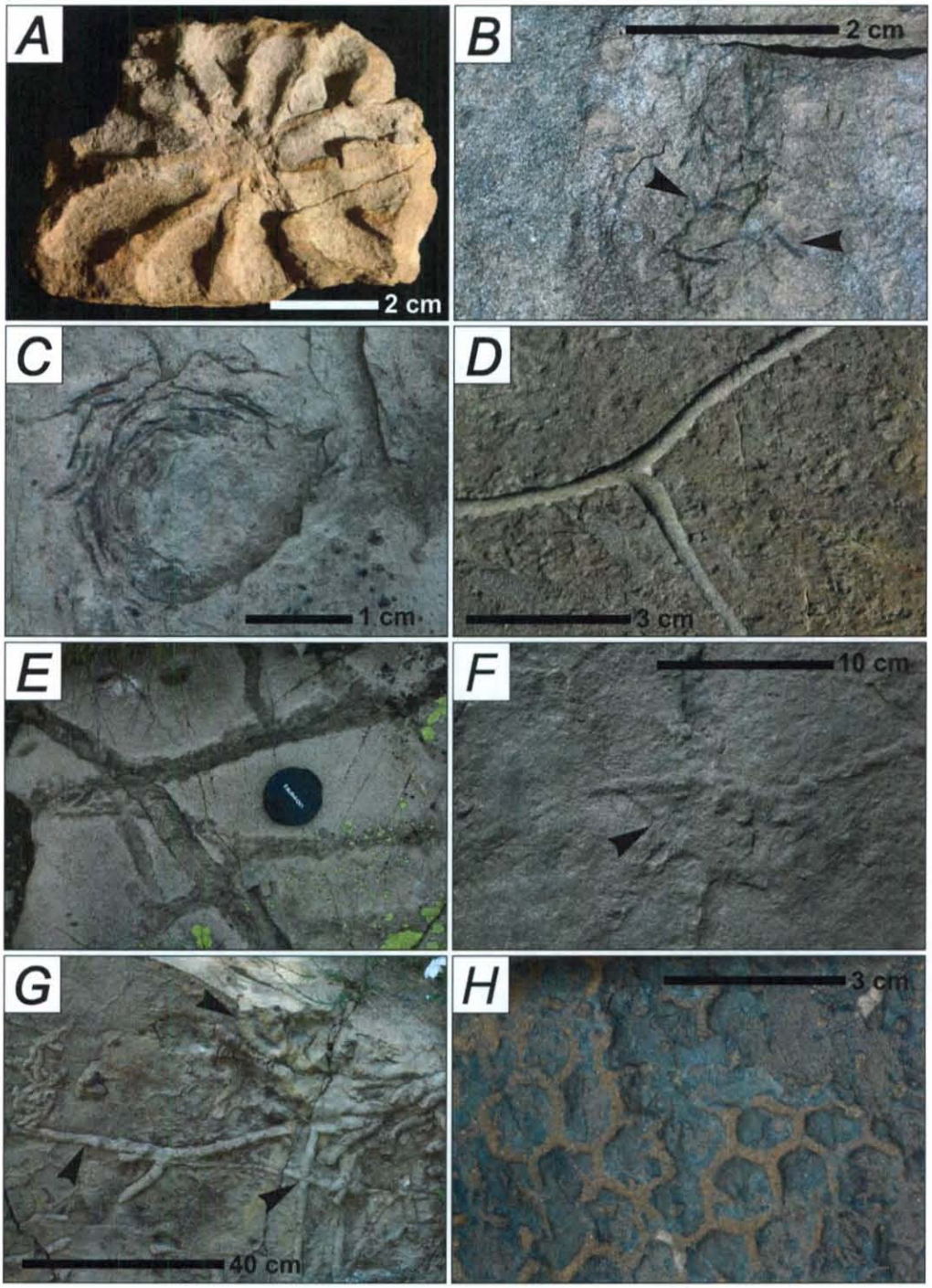
2.4.1. ?*Asterosoma* von Otto, 1854

?*Asterosoma radiciforme* von Otto, 1854

Plate 2.1A

Description: One collected specimen; composed of eleven concave rays (depressions in the substrate surrounded by ridges of sediment) radiating from a central point, parallel to bedding plane. Rays are 14–30 mm long and widen away from the central point, from 1–3 mm to 5–10 mm. Whole specimen is 60 mm wide. The depressions are here interpreted to be lower part of radiating spindle structures typical of *Asterosoma* which has been weathered out preserving a mould of the burrow.

Palaeoenvironmental interpretation: *Asterosoma* is a common trace fossil reported from marginal marine to deep marine environments (Chamberlain, 1978; MacEachern & Hobbs, 2004; Neto de Carvalho & Rodrigues, 2007). *Asterosoma* has been interpreted as the dwelling burrow of a decapod crustacean (Häntzschel, 1975). It has also been suggested that *Asterosoma* represents the deposit feeding burrow of vermiform organism (Pemberton *et al.*, 2001).


A
2 cm
B
2 cm
C
1 cm
D
3 cm
E
F
10 cm
G
40 cm
H
3 cm

2.4.2. Chondrites von Sternberg, 1833

Chondrites isp.

Plare 2.1B

Description: Regularly-branched tunnels, less than 1 mm thick. Branches are straight and bifurcate at angles between 45–90°. Found in sandstone, filled with mudstone. Preserved on upper bedding surfaces.

Palaeoenvironmental interpretation: *Chondrites* is a facies-crossing trace fossil found in a variety of depositional settings (Bromley, 1996; Buatois *et al.* 2007). Many authors have found *Chondrites* in beds associated with lowered oxygen levels (Bromley & Ekdale, 1984; Ekdale & Masson, 1988). Finding *Chondrites*, however, should not be taken as an unequivocal indicator of either seafloor dysoxia or pore water anoxia. In settings where it is the only ichnotaxon present (e.g. in black shales) it is considered to be an indicator of physiologically stressed marine environments, probably with highly sulfidic pore waters (Bromley & Ekdale, 1984; Savrda & Bottjer, 1986; Wetzel & Uchman, 2001; MacEachern *et al.* 2007b). The structure is considered to represent complex deposit feeding (Ekdale, 1977; Pemberton *et al.* 2001). Alternatively, *Chondrites* is thought to be the feeding burrow of a chemosymbiotic vermiform animal (Seilacher, 1990) living at depth in the sediment, probably below the redox boundary.

2.4.3. Diopatrichnus Kern, 1978

Diopatrichnus isp.

Plate 2.1C

Description: Shell-lined vertical tubes. Appear circular and sub-circular in cross section, 1.5–2.0 cm wide. Unbranched. Only found on bedding planes. Bivalve shell fragments which constitute the burrow wall are concentrically lined. Burrow fill is structureless.

Palaeoenvironmental interpretation: *Diopatrichnus* is considered to be the trace fossil of a tube-building polychaete worm similar to the onuphid *Diopatra* (Gibert, 1996). *Diopatra* has been recorded in water depths to 222 m from California to South America in areas of moderate to strong current energy (Kern, 1978).

2.4.4. Ophiomorpha Lundgren, 1891

Ophiomorpha is a commonly occurring trace fossil. It is a three-dimensional, deep burrow network made of sub-cylindrical to cylindrical burrows. Horizontal galleries are connected to the sediment-water interface by vertical shafts which may be over 1 m long (Uchman, 2009). Burrows are commonly branched with Y- or T-shaped bifurcations. Junctions may be swollen to allow the tracemaker to turn in its burrow (Frey *et al.* 1978). Burrow walls are internally smooth. External wall may be mamillate with small discoid or ovoid pellets partially or completely lining the burrow (Bromley and Pedersen, 2009; McIlroy *et al.* 2009). *Ophiomorpha* has been found from the Permian to the Recent (Swinbanks and Luternauer, 1987). The *Ophiomorpha*-producing animal is most likely a crustacean similar to modern thalassinid shrimps. Members of the genus *Callianassa*,

Neotrypaea, and *Upogebia* are found in shoreface to offshore environments and construct *Ophiomorpha*-style burrows (Weimer & Hoyt, 1964; Frey *et al.* 1978). *Ophiomorpha* is a facies-crossing trace fossil not restricted to any single depositional environment or lithology. It is commonly found in high energy shoreface environments (Pemberton *et al.* 2001). Some species of *Ophiomorpha*, specifically *O. rudis*, are common in deep marine palaeoenvironments (Uchman, 2001, 2009). The *Ophiomorpha*-making organism is interpreted to range from deposit feeding to suspension feeding to farming (Bromley, 1996). *Ophiomorpha* is considered to be the burrow of a highly adaptive and opportunistic group of organisms which make palaeoenvironmental interpretation challenging.

2.4.4.1. Ophiomorpha annulata Książkiewicz, 1977

Plate 2.1D

Description: Vertical shafts and more common horizontal tunnels on turbidite soles. Burrows 5–7 mm wide. Y-shaped branches common. With or without a pelleted wall but always lined. Mudstone pellets ~2 mm wide, regularly spaced.

Palaeoenvironmental interpretation: *O. annulata* is a common trace fossil in deep-water facies found in turbidite successions (Uchman, 2001). This ichnospecies of *Ophiomorpha* is thought to reflect deposit-feeding activity of small crustaceans (Uchman *et al.* 2004).

2.4.4.2. Ophiomorpha ?nodosa Lundgren, 1891

Plate 2.1E

Description: Horizontal tunnels, 30–50 mm wide. Wall is made of discoid mudstone pellets, regularly spaced, ~10 mm wide. T- and Y-shaped branching characterizes the galleries.

Palaeoenvironmental interpretation: *O. nodosa* has long been thought of as the dwelling structure of a burrowing shrimp due to its morphological similarity to modern-day burrows of *Callichirus* (formerly *Callianassa*) *major*, a shoreface and shallow-water mud shrimp. The modern burrow of *C. major* has a mamillate wall and dimensions similar to that of *O. nodosa* (Weimer & Hoyt, 1964; Frey *et al.* 1978; Bromley, 1996). *O. nodosa* is a common trace fossil in estuarine and near shore environments (Miller & Curran, 2001; Pemberton *et al.* 2001). This ichnospecies is generally recorded from sand-rich palaeoenvironments (Pollard *et al.* 1993). Finding *O. ?nodosa* in turbidites is atypical as it is usually considered to be a shallow-water ichnospecies.

2.4.4.3. Ophiomorpha rudis Książkiewicz, 1977

Plate 2.1F-G

Description: Sub-cylindrical tunnels and shafts 10–30 mm wide. Burrows are straight or curved, filled with mud or sand. Burrow walls are made of disc-shaped mudstone pellets 3–7 mm long. Pellets may completely or partially cover the wall. Burrows have T-shaped bifurcations. Swellings observed at many junctions. Some specimens have very large swellings from which multiple tunnels emerge (Plate 2.1F). Some *O. rudis* are

actively backfilled (Plate 2.4B). Deep-penetrating burrows, some >2 m in length are documented here (Plate 2.3F).

Palaeoenvironmental interpretation: *O. rudis* is environmentally diagnostic of sandy deep-water environments (Uchman, 2001, 2009). It is common in deep-sea proximal fan lobes as well as channels and channel margins (Uchman, 2001). The *Ophiomorpha rudis* ichnosubfacies of the *Nereites* ichnofacies was erected for its occurrence in these sand-rich, high current energy settings (Uchman, 2001, 2009). The *O. rudis* animal is considered to be predominantly a deposit feeder, feeding on organic matter or from microbes cultured in organic-rich facies (Uchman, 2009). As with many burrows, other facultative behaviours may occur in the same burrow (Herringshaw *et al.*, 2010). The ability to penetrate great thicknesses of sediment is considered to be an adaptation of the animal to exploit deeply-buried organic carbon-rich inter-turbidite mudstones.

2.4.5. Paleodictyon Meneghini, 1850

Paleodictyon majus Meneghini in Peruzzi, 1880

Plate 2.1H

Description: Honeycomb-like network of hexagonal polygons, complete or incomplete convex mesh-like structure. Polygons 8–12 mm in diameter. Casts of burrows 0.9–1.0 mm wide. Found in irregularly shaped patches, 10 cm wide. Randomly distributed on the bedding plane.

Palaeoenvironmental interpretation: *Paleodictyon* is a deep-water trace fossil thought to be constructed for trapping meiobenthic organisms or cultivating micro-organisms within

the sediment (Seilacher, 1977). The lack of scratch marks on the burrow wall has been used to suggest that the substrate was soft at the time of burrowing (Wetzel & Uchman, 1997). The lack of bioglyphs could also suggest that the organism had neither setae nor burrowing appendages. *Paleodictyon* is indicative of deep marine oligotrophic waters from the Lower Palaeozoic to the Recent (Uchman, 2003). It is only preserved in comparatively quiescent palaeoenvironments where low-frequency, slow, or distal (usually turbiditic) events sand-cast the burrows immediately after exposure by erosion (Seilacher, 1977; Orr, 1995).

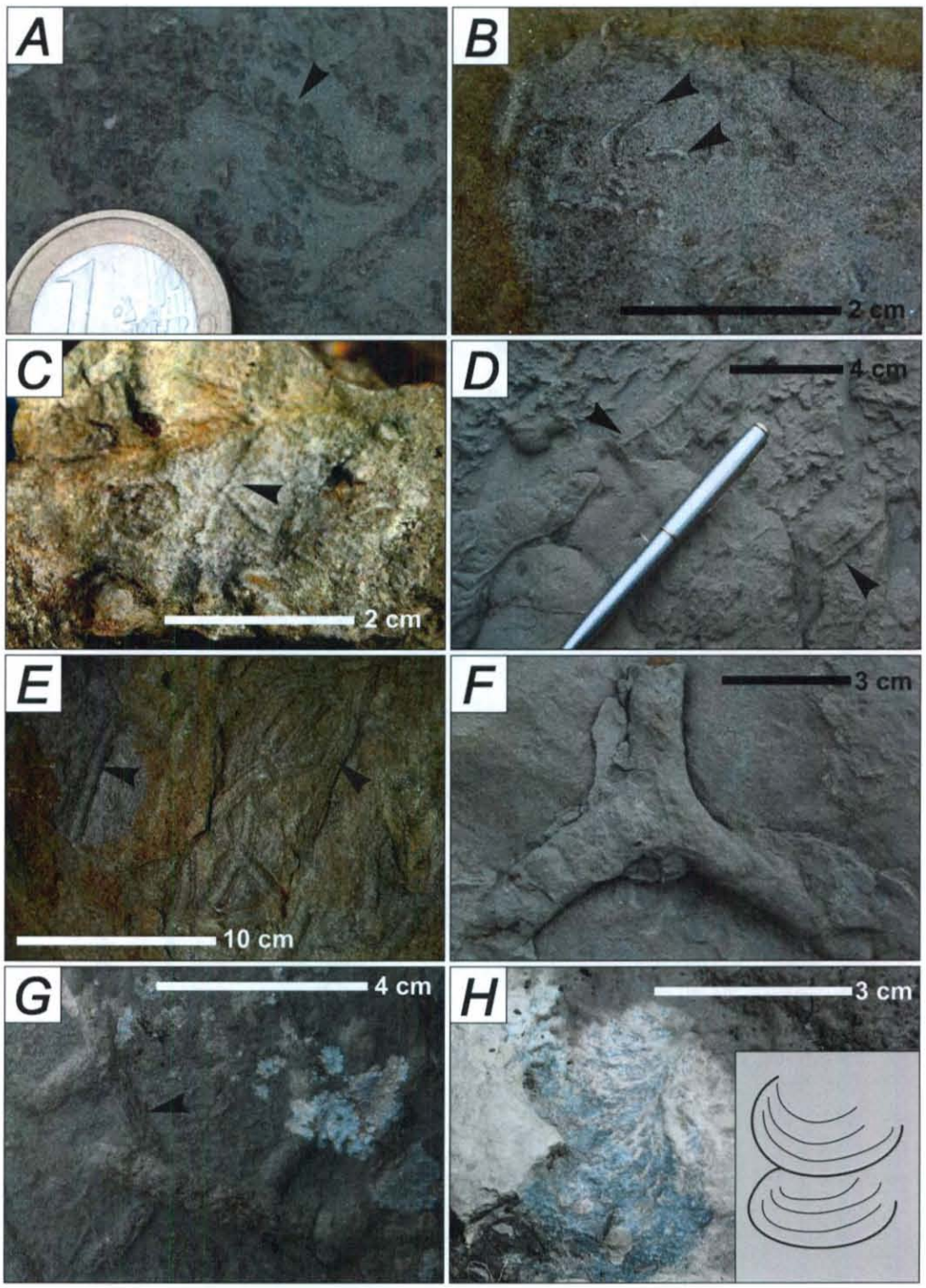
2.4.6. Phycodes Richter, 1850

Phycodes isp.

Plate 2.2A

Description: Numerous smoothly curved lateral branches from a master stem producing bunches of burrows on one side. Individual side branches 5 mm wide. Whole specimen, 30 mm long. This matches the description of *Phycodes* as "flabellate or broomlike are developed from a single or few initial (or proximal) tunnels" (Han & Pickerill, 1994, p. 37).

Palaeoenvironmental interpretation: *Phycodes* is a facies-crossing ichnogenus found from shallow marine (Schlirf, 2000) to deep marine environments (Han & Pickerill, 1994; Miller, 2001). *Phycodes* is common trace fossil in the Phanerozoic shallow marine but is less common in deep marine and non-marine palaeoenvironments (Han & Pickerill,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1994). It is made by endobenthic deposit feeding organisms with systematic, bedding parallel, probing behaviour.

2.4.7. Phycosiphon Fischer-Ooster, 1858

Phycosiphon isp.

Plate 2.2B

Description: Meandering tubes arranged in an antler pattern characterized by incomplete hook-shaped burrows enclosing poorly preserved spreite. Found parallel to bedding. Burrow 1–2 mm wide. Filled with a paler material than host sediment. Found parallel to bedding in patches 10 cm wide.

Palaeoenvironmental interpretation: *Phycosiphon* is another facies-crossing ichnogenus constructed by the deposit feeding activity of a vermiform organism. It is found in a variety of depositional settings from lower shoreface to bathyal environments (Wetzel & Bromley, 1994). *Phycosiphon* is most often found cross-cut by other ichnogenera in new turbidites implying that the progenitor was one of the first organisms to colonize the sediment (Wetzel & Uchman, 2001). This suggests an opportunistic organism found within deep marine or deep-shelf sediments (Uchman *et al.* 2004). *Phycosiphon* has been found associated with dysoxic environments in low diversity monospecific assemblages (Ekdale & Mason, 1988). Recent *Phycosiphon* has been found at abyssal depths (below 4400 m) in the Sulu Basin, Philippines, in settings subjected to low bottom water oxygenation and high sedimentation rates (Wetzel, 1983; Wetzel & Bromley, 1994).

2.4.8. Planolites Nicholson, 1873

Planolites isp.

Plate 2.2C

Description: Unlined, straight or gently curved horizontal, circular to sub-circular burrows, 1–3 mm wide. T-shaped branching occasionally seen. Most are unbranched. Burrow fill is structureless and composed to the same material as the host rock.

Palaeoenvironmental interpretation: *Planolites* has been found in a wide range of palaeoenvironments from soils and freshwater settings to the deep marine (Keighley & Pickerill, 1995; Pemberton *et al.* 2001). An abundance of *Planolites* is indicative of well oxygenated bottom waters in shallow marine settings (Bromley, 1996) while low abundances have been inferred to result from lowered bottom water oxygen levels. It is thought to have been formed by a vermiform organism (Häntzschel, 1975; Pemberton *et al.* 2001).

2.4.9. Scolicia de Quatrefages, 1849

Scolicia prisca de Quatrefages, 1849

Plate 2.2D-E

Description: A trilobate structure consisting of one central lobe of either poorly preserved or structureless material 2–20 mm wide separating two parallel strings 1 mm wide. Gentle to tightly meandering structures found parallel to the bedding. Can occur in high-density patches (Plate 2.2E).

Palaeoenvironmental interpretation: *Scolicia* is a facies-crossing trace fossil documented from a range of depositional settings (Uchman, 1995a; Tchoumatchenco & Uchman, 2001). *Scolicia* is interpreted as a grazing trace produced by irregular echinoids (Uchman, 1995a) commonly found in sand-rich environments (Wetzel & Uchman, 2001). The two parallel strings indicative of some ichnospecies of *Scolicia* have been interpreted as the casts of drainage tufts of spatangoid echinoids (Uchman, 1995a). *Scolicia prisca* is found in Bouma turbidite divisions T_{cd} in the transition between sandstones and mudstones (Uchman, 1995a, 1998). It has been noted that the *Scolicia* organism is tolerant of porewater anoxia in that they are thought to utilize endosymbiotic sulphur-oxidizing bacteria and are usually found close to the redox boundary (Bromley *et al.* 1995).

2.4.10. Thalassinoides Ehrenberg, 1944

Thalassinoides suevicus Rieth, 1932

Plate 2.2F-G

Description: Cylindrical to sub-cylindrical burrows, 15–30 mm wide, seen as vertical shafts up to 1 m long branching horizontally with Y-shaped bifurcations and junction swellings. Burrows are unlined. Burrow fill is structureless. Tunnels have tightly packed longitudinal grooves, less than 1 mm wide (Plate 2.2G).

Palaeoenvironmental interpretation: *Thalassinoides* is a common trace fossil from the Ordovician to Recent (Swinbanks & Luternaur, 1987). It is a facies-crossing ichnogenus documented from the shallow marine (Pemberton *et al.* 2001) and, less frequently, the

deep marine (Uchman, 1998). A non-lithified stable substrate is needed for the preservation of the burrows (Schlirf, 2000) and a firm substrate is needed for the preservation of bioglyphs (seen as longitudinal grooves) which were made by the burrowing animal scratching the interior wall of the burrow (Frey *et al.* 1978). Lithology is not a controlling factor on the distribution of *Thalassinoides*. It has been documented from sandstones and mudstones and from firmgrounds where *Thalassinoides* is a constituent of the *Glossifungites* ichnofacies (MacEachern *et al.* 1991; Martin & Pollard, 1996). The burrow is generally interpreted to be formed by crustaceans (Frey *et al.* 1984). The Grès d'Annot *Thalassinoides* is interpreted as a deposit feeder that burrowed through thick sandstone turbidites, before branching horizontally along mudstone-sandstone interfaces. It is inferred that this behaviour reflects the search for organic carbon-rich inter-turbidite mudstones.

2.4.11 Zoophycos Massalongo, 1855

Zoophycos isp.

Plate 2.2H

Description: Two stacked whorls filled with poorly-preserved laminae, each lamina-set (or spreiten) preserves the previous position of the active burrow as the organism mined the sediment in a radial manner. The *Zoophycos* found within the Grès d'Annot Formation is morphologically comparable with the Eocene *Zoophycos* described by Seilacher (2007).

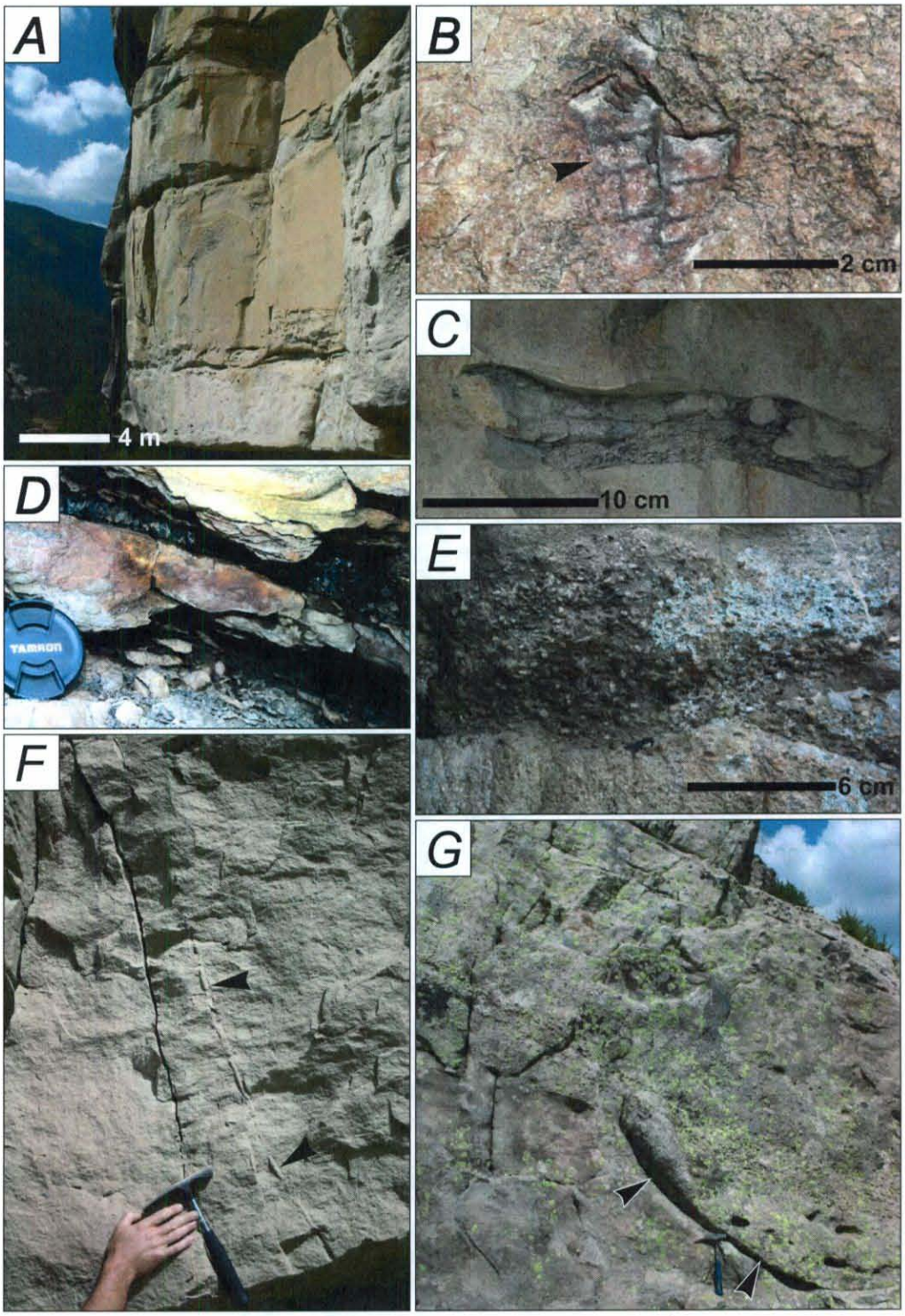
Palaeoenvironmental interpretation: *Zoophycos* is found from the Ordovician to the Recent (Seilacher, 2007). It is interpreted as the burrow of an efficient deposit feeding animal. It appears to be abundant during periods of quiescence of the seafloor (Pemberton *et al.*, 2001). It is found in association with *Chondrites* during dysoxic intervals (Bromley & Ekdale, 1984). *Zoophycos* is inferred to be produced by an opportunistic organism capable of exploiting oxygen-depleted environments (Bromley, 1996). The ethology of the *Zoophycos* tracemakers is debatable. Some authors consider the burrowers to be detritus feeders (Kotake, 1989). It has been suggested that the burrow was used for culturing micro-organisms (Fu & Werner, 1995). This has been questioned based on the minimal difference in $\delta^{13}C_{org}$ values between *Zoophycos* spreiten and host sediment with a food cache burrow model suggested in place of gardening (Löwemark *et al.* 2007). Modern examples of *Zoophycos* have been found in slope and rise sediments from the Sulu Basin in the Philippines (Wetzel, 1983) and in water depths of >2 km off the NW African continental slope (Wetzel & Werner, 1981).

2.5. Sedimentary facies

2.5.1. Sand-dominated facies

2.5.1.1. Facies 1

Description: This facies consists of thick (50 cm to >5 m) coarse- to fine-grained sandstone beds (Plate 2.3A) that are either massive or normally graded. Fragments of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leaves and plant stems can be found on upper surfaces (Plate 2.3B). A distinctive feature of this facies is the presence of bioturbated mudstone intraclasts (Plate 2.3C) which are randomly distributed. Flute casts occur on the soles of some beds while other bedding surfaces show no discernable erosion and are planar and undisrupted at outcrop scale.

Ichnology: BI 0–1. *Ophiomorpha rudis*, and less common *Thalassinoides suevicus*, are observed. Vertical shafts of *O. rudis* are seen penetrating beds >2 m thick (Plate 2.3F). Some of the mudstone intraclasts are intensely bioturbated by *O. rudis* (Plate 2.3C).

Interpretation: Facies 1 was deposited in a deep-water setting from concentrated, sand-rich turbidity currents. These currents probably encountered an obstacle to flow or a decrease in slope gradient leading to rapid deceleration. Such conditions led to ponding and rapid deposition of massive sandstone beds. Consequently, only deep burrows like *O. rudis* and *T. suevicus* are preserved.

2.5.1.2. Facies 2

Description: This facies consists of fine- to medium-grained sandstone beds 2–40 cm thick. Physical sedimentary structures include planar parallel, wavy, and convolute lamination. Alternatively, these sandstones can be massive. Rare coalified wood clasts, 10–30 cm long, are randomly distributed and recorded basin-wide (Plate 2.3D). The coalified clasts are unbioturbated.

Ichnology: BI 0–2. This facies contains an abundant but unevenly distributed ichnological assemblage including *Chondrites* isp., *Ophiomorpha rudis* and *O. annulata*, *Paleodictyon majus*, *Phycodes* isp., *Planolites* isp., and *Thalassinoides suevicus*.

Interpretation: This facies is composed Bouma T_b divisions (massive sandstone) with Bouma T_c divisions (parallel and convolute laminated sandstone) deposited under low flow regime conditions. Lower hydrodynamic energy conditions allowed preservation of a more diverse ichnofaunal assemblage.

2.5.1.3. Facies 3

Description: Very coarse-grained sandstones and conglomeratic sandstones are characteristic of this facies. The beds are normally graded or massive and may be amalgamated into 7 m thick sandstone successions. The sandstones typically have coarse-grained basal lags (Plate 2.3E). This facies differs from facies 1 in being very much coarser with pronounced basal lags to beds. The coarse-grained pebbly lags can be demonstrated to fill flute-like scours 30 cm to >1 m wide and 5–60 cm deep (Plate 2.3G). The facies is described from the Col de la Cayolle area only.

Ichnology: This facies is poorly bioturbated (BI 0–1) with a low diversity trace fossil assemblage. Shafts of *Ophiomorpha rudis* are uncommon and occur with rare *O. ?nodosa.*

Interpretation: It is inferred to have been deposited from high volume and high concentration flows. Although not proximal to the source area, the Col de la Cayolle area could have been supplied with this very coarse material directly during high concentration, high volume turbidite events. The depositing currents are inferred to have been highly turbulent as suggested by the presence of scour-and-fill structures. These depositional conditions are inconducive to shallow burrow preservation. Only deep penetrating *Ophiomorpha* ichnospecies are documented from this facies.

2.5.1.4. Facies 4

Description: This facies is composed of medium- to very coarse-grained sandstone beds 1–2 m in thickness. No tractional sedimentary structures are present in the beds which display a chaotic internal structure. Intraclasts are common and are distributed throughout the bed.

Ichnology: No trace fossils were described from this facies.

Interpretation: The sandstones of this facies are interpreted to have been debrites deposited as a result of slope failures on a confining slope or at a channel margin. This facies is only recorded from the Braux outcrop.

2.5.2. Heterolithic facies

2.5.2.1. Facies 5

Description: This heterolithic facies is composed of thin- to medium-bedded (5–40 cm in thickness) successions of interbedded claystones, siltstones, and very fine- and fine-grained sandstones (Plate 2.4A). The claystones and siltstones have either parallel and convolute laminae or can be homogeneous. Sandstone beds have a range of sedimentary structures including asymmetrical ripple cross laminae, planar parallel laminae, and convolute laminae. The mudstone to sandstone ratio in this facies is typically 1:3. There is neither a discernible cyclicity to these bed thicknesses, nor trend in mud to sand ratio.

Ichnology: *Ophiomorpha rudis* and *O. annulata* dominate this facies with *Chondrites* isp., *Paleodictyon majus*, *Planolites* isp., *Thalassinoides suevicus*, and *Zoophycos* isp. also present.

Plate 2.4. (Overleaf). Field images of heterolithic and mud-dominated facies.

A. Facies 5. A heterolithic succession of medium- and thin-bedded turbidites and inter-turbidite mudstones. Field assistant for scale. Montagne de l'Avalanche, Col de la Cayolle.

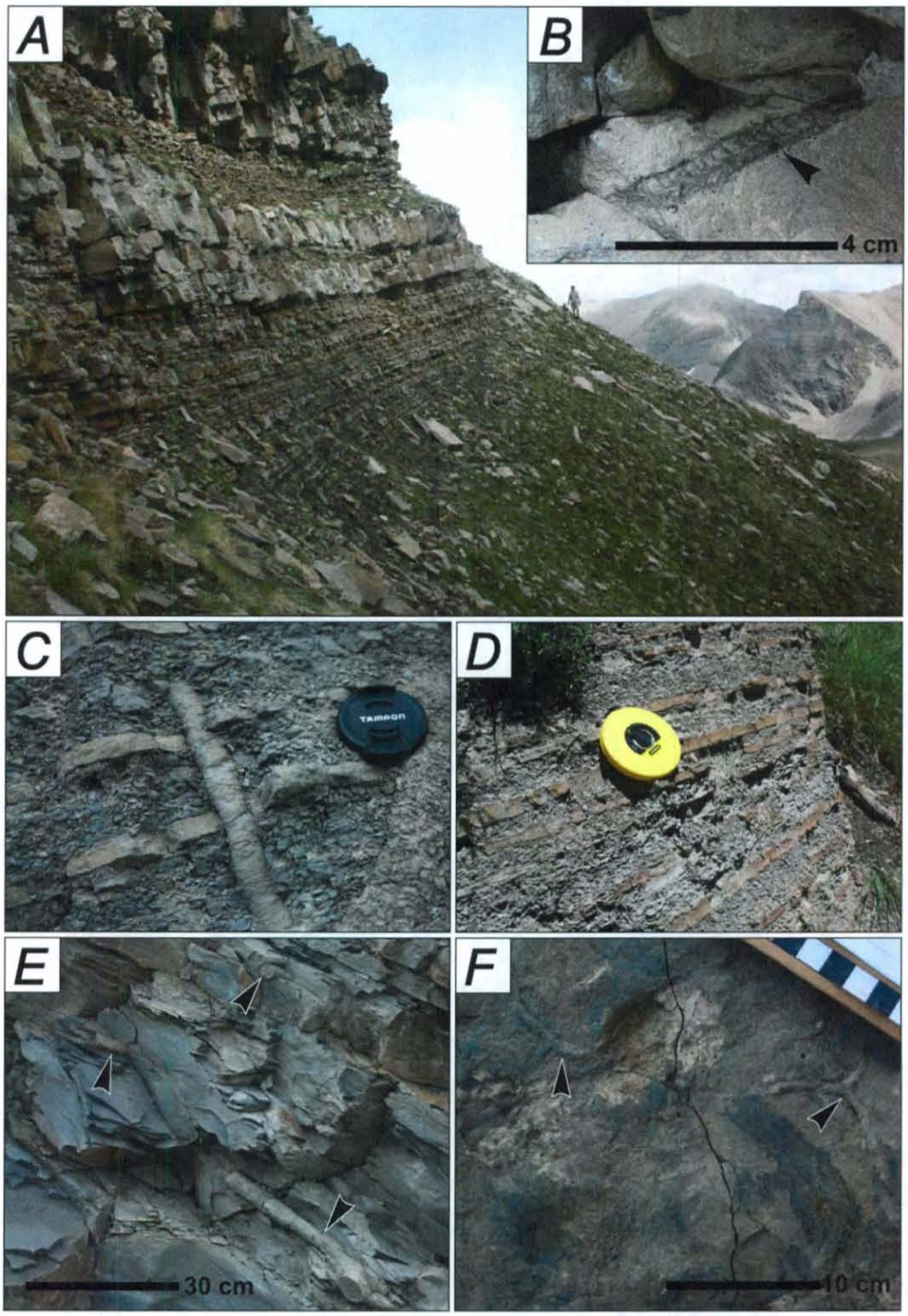
B. Facies 5. *Ophiomorpha rudis* with meniscate backfill from the outcrop shown in A.

C. Facies 6. *Ophiomorpha rudis* penetrating thin-bedded turbidite beds. Lens cap is 5 cm wide. Braux.

D. Facies 6. Sandstones interbedded with fine-grained turbidite material and hemipelagite. Measuring tape is 20 cm wide. Argenton.

E. Facies 7. Medium-bedded inter-turbidite claystone with numerous *Ophiomorpha rudis* (arrowed). Baisse de l'Aiguille.

F. Facies 7. *Ophiomorpha rudis* on top of an inter-turbidite claystone forming open polygons. Baisse de l'Aiguille.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Interpretation: This facies is only found in the Col de la Cayolle area. The heterolithic beds are in sharp non-erosive contact with the thick-bedded turbidites of facies 1 and facies 3. They are interpreted as the deposits of low velocity and low concentration turbidity flows deposited as thin-bedded unconfined turbidites. This facies is underlain by thick-bedded and coarse-grained sand-rich turbidites (facies 1 and 3). This change in deposition is considered to represent channel abandonment with thin- to medium-bedded turbidites filling accommodation space. The ichnotaxa present are inferred to represent the burrows of a deposit-feeding community of organisms. Burrows are concentrated at sand-mud interfaces and within mudstones with the exception of *Paleodictyon* which probably represents microbe farming in mud-rich sediments at depths of approximately 2 mm (Seilacher, 1977).

2.5.2.2. Facies 6

Description: This facies is characterized by thin- to medium-bedded, very fine-grained sandstone or siltstone turbidites with mudstone interbeds. Fining-upward cycles of 10+ or even 30+ rhythmic beds with clear cyclicity are observed (Plate 2.4D). The very fine sandstone or siltstone units are calcite cemented. These beds are 5–30 cm thick with parallel, wavy, or convolute lamination. Deposited on top of these are homogeneous, calcareous claystones 5–40 cm thick.

Ichnology: BI 0–3 in the sandstone/siltstone unit. The claystone has a BI 6 as it has been completely homogenized. *Phycosiphon* isp. is the most volumetrically dominant trace fossil in this facies. *Ophiomorpha annulata* and *O. rudis* are also common, with accessory ?*Asterosoma radiciforme*, *Planolites* isp., and *Scolicia prisca*.

Interpretation: Facies 6 is found exclusively on intra-basin slopes that onlapped during deep-basin sedimentation. It is interpreted to have been deposited from decelerating, relatively low concentration, turbidity currents and is representative of the Marnes Brunes Inférieures Formation. The claystones are thought to be a bioturbated mixture of clay-grade turbidite and hemipelagic material. Low hydrodynamic energies generated from low volume flows allow preservation of a diverse ichnofauna while fine-grained, possibly nutritious, material could support have supported the increased benthic diversity recorded.

2.5.3. Mud-dominated facies

2.5.3.1. Facies 7

Description: Thin- to medium-bedded, siltstones and claystones are characteristic of this facies. The dominant lithology is claystone with minor siltstone horizons. The facies can be parallel laminated or massive (Plate 2.4E). Facies 7 is found basin-wide.

Ichnology: BI 2–6. Ichnodiversity is low with only post-depositional, deep *Ophiomorpha rudis* and *Thalassinoides suevicus* recorded. In some areas this facies is burrowed solely by *O. rudis* in high density monospecific assemblages.

Interpretation: This facies represents a burrow-homogenized mudstone deposited from waning, relatively dilute, turbidity currents and background sedimentation in the deep basin. These subsequently buried inter-turbidite units were a significant source of nutrition for deep-burrowing tracemakers as near-surface environments appear to have been nutrient-deficient.

5.3.2. Facies 8

Description: This facies consists of blue, massive, calcareous claystones. It is distributed basin-wide.

Ichnology: *Diopatrichnus* isp. is the only ichnotaxon recorded from this facies (Plate 2.4D).

Interpretation: This facies is the Marnes Bleues Formation, which is thought to have been deposited on a slope or distal ramp setting from the Priabonian to the Lower Oligocene based on micropalaeontological determinations of Bouroulloc *et al.* (2004).

2.6. Ichnofabrics

Ichnofabrics are described as "those aspects of the texture and internal structure of the bed resulting from all phases of bioturbation" (Ekdale & Bromley, 1983, p. 110). Ichnofabrics documented from the Grès d'Annot Basin are *Ophiomorpha*-dominated reflecting the abundance and/or productivity of the producing organism in the basin during turbidite deposition. Ichnofabrics are volumetrically dominated by large *Ophiomorpha rudis* with variable proportions of other, less prominent, trace fossils. Modified ichnofabric constituent diagrams (Taylor & Goldring, 1993; McIlroy, 2004a) were produced for all of the ichnofabrics documented (Fig. 2.3). Owing to significant potential for patchiness of ichnofabric, the approach of producing ichnofabric associations is followed herein (McIlroy, 2007). These ichnofabrics are facies-controlled (i.e., each ichnofabric is found in a limited number of facies).

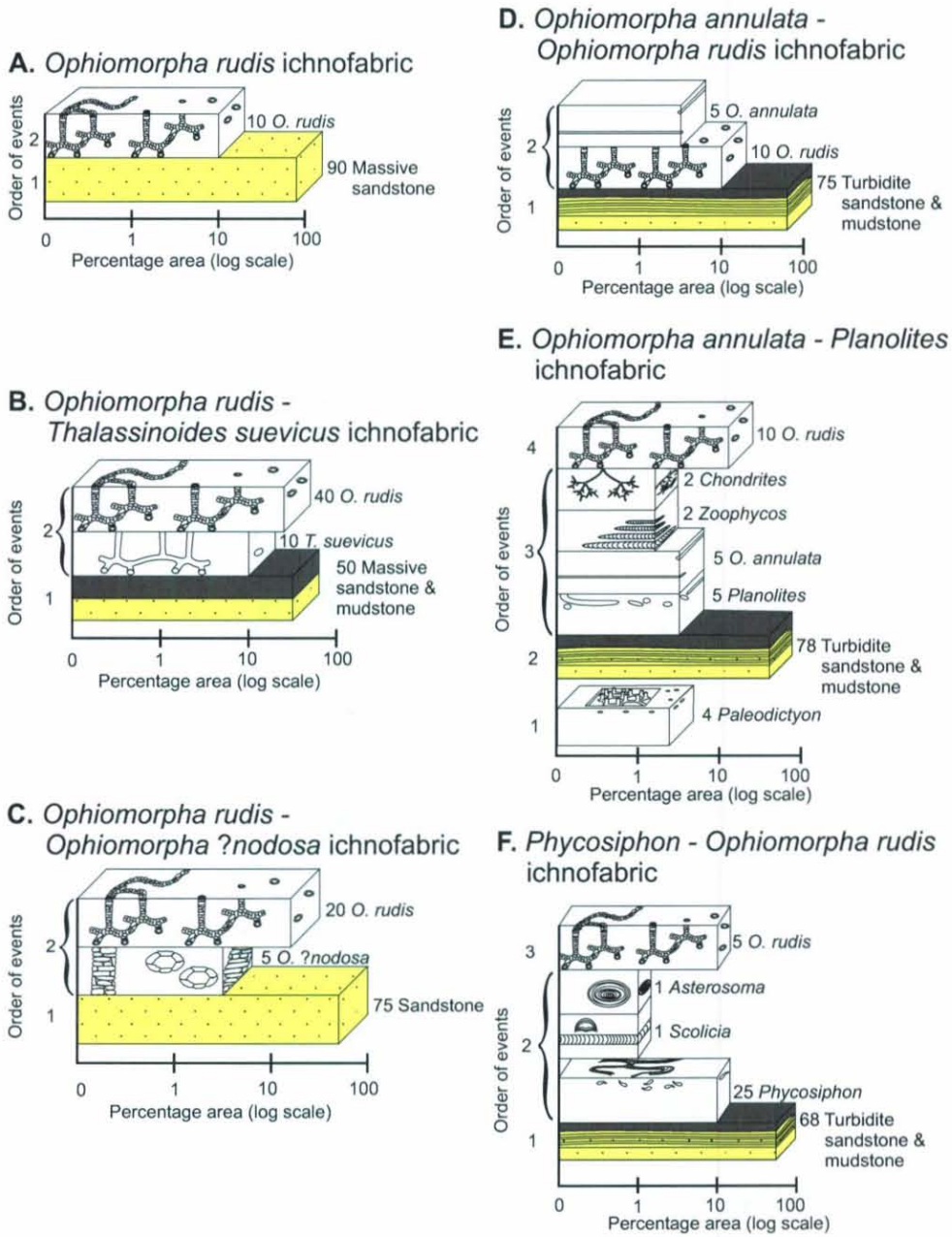


Fig. 2.3. Ichnofabric constituent diagrams for three ichnofabric associations and six ichnofabrics documented. The vertical axis indicates the order of events starting with either pre-turbidite ichnotaxa or turbidite deposition followed by colonization by post-depositional ichnotaxa. Numbers associated with each event indicate the percentage (by area) of the ichnofabric constituted by each event.

2.6.1. The Ophiomorpha rudis ichnofabric association

This association is defined by the abundance of *Ophiomorpha rudis*, the commonest trace fossil in facies 1, 3, and 7. *O. rudis* is the most abundant ichnotaxon volumetrically and by a bedding plane bioturbation index (Miller & Smail, 1997).

2.6.1.1. *Ophiomorpha rudis* ichnofabric

This ichnofabric is observed throughout the Grès d' Annot Basin in thick- and thin-bedded massive sandstones and their associated mudstones. The ichnofabric consists exclusively of vertical shafts and/or horizontal tunnels of *Ophiomorpha rudis*. In the thick-bedded sandstone turbidites of facies 1, *O. rudis* penetrates thick layers of sediment down to sand-mud interfaces more than 2 m below the colonization surface (Plate 2.3F). Some sandstone soles show numerous burrows; with abandoned burrows being cross-cut by active ones (Plate 2.1H). In facies 7, extensive horizontal galleries of *O. rudis* were found to cover up to 50% of the surface area of exposed surfaces. *O. rudis* in this setting is inferred to have been deposit feeding either on organic matter and/or microbes in the fine-grained sediment (following Uchman, 2009).

Ophiomorpha rudis galleries are also found in association with coarse-grained bed tops in the thick-bedded sandstones of facies 3. These features are inferred to result from current-winnowing turbidity currents carrying away fine-grained material and leaving a lag of coarser grained sand and gravel behind. The *Ophiomorpha* animals in these situations are interpreted to have employed a suspension feeding mode of life, extracting

nutrients from persistent currents rather than burrowing to find organic carbon-rich layers below.

2.6.1.2. *Ophiomorpha rudis-Thalassinoides suevicus* ichnofabric

The massive claystones of facies 7 have a low ichnodiversity. *O. rudis* is recorded in high abundance with *T. suevicus* as an accessory trace fossil. Burrows extend from bed tops to bed soles, a thickness of 10–50 cm. *O. rudis* is also seen as irregular, incomplete polygons on the top surface of claystone beds (Plate 2.4F). This expression of *O. rudis* is documented from other localities where the tracemaker constructs large boxwork-style burrows in the sediment (Uchman, 2009). The beds that contain this ichnofabric have no primary sedimentary fabric; the matrix is burrow mottled. The trace fossils within this ichnofabric are inferred to represent a dense community of deposit-feeding crustaceans. The *Ophiomorpha* organisms most likely burrowed down from the colonization surface to feed on the pre-turbidite organic carbon-rich layers.

2.6.1.3. *Ophiomorpha rudis-Ophiomorpha ?nodosa* ichnofabric

This is found within coarse-grained channelized sandstones with very-coarse-grained lags and scours. This ichnofabric is only found associated with facies 3 and is very rare. The trace fossils are present in low abundance assemblages in massive sandstone beds approximately 2 m thick massive sandstone beds. *Ophiomorpha rudis* is the dominant trace fossil in the assemblage while rare *O. ?nodosa* form horizontal galleries on the tops of sandstone turbidites. This ichnofabric is inferred to have been produced by burrowing crustaceans with a deposit-feeding mode of life in settings with a high hydrodynamic

energy, possibly with shifting sands. This is inferred from the close morphological similarities between *O. nodosa* and the burrow of a modern progenitor, *Callichirus major*, which lives in high current energy settings such as estuaries, shoreface, and nearshore environments (Wiemer & Hoyt, 1964).

2.6.2. The Ophiomorpha annulata ichnofabric association

The ichnofabrics of the *Ophiomorpha annulata* ichnofabric association are dominated by *O. annulata* at sandstone-mudstone interfaces in heterolithic successions of thin-bedded turbidites.

2.6.2.1. *Ophiomorpha annulata-Ophiomorpha rudis* ichnofabric

This ichnofabric is found in the fine-grained, massive or parallel laminated sandstone and mudstone beds of facies 2 and 5. Trace fossils are seen as vertical shafts and as interface burrows at both sand-sand and sand-mud contacts. *O. annulata* and *O. rudis* are found to be mutually cross-cutting and no systematic succession of colonization is inferred. This ichnofabric is found in much of the Grès d'Annot Formation in sandstone beds interpreted to be formed in association with low volume turbidity current events.

2.6.2.2. *Ophiomorpha annulata-Planolites* ichnofabric

Successions of thin-bedded, fine-grained sandstone turbidites and inter-turbidite siltstones and claystones are commonly dominated by *O. annulata* and *Planolites*. Both these trace fossils are abundantly represented by narrow tunnels at sand-sand, sand-mud, and mud-

mud contacts. This ichnofabric is associated with facies 5, and is indicative of a low-energy hydrodynamic regime. Low flow-regimes and infrequent, weakly erosive turbidite events are also inferred from the presence of *Paleodictyon*. Deep burrows such as *Chondrites* and *Zoophycos* are present but rare. *Ophiomorpha rudis* is found in this heterolithic facies but is less common than in the ichnofabrics associated with sand-rich facies.

2.6.3. The Phycosiphon-Ophiomorpha rudis ichnofabric

In this ichnofabric, *Phycosiphon* is the most abundant trace fossil. It occurs as shallow-tier pervasive burrows found in small patches on the bedding planes of thin-bedded turbidites. *Ophiomorpha rudis* may penetrate multiple turbidite beds (Plate 2.4C) but a colonization surface could not be unequivocally identified to determine the maximum depth of burrowing (which can be greater than 2 m below the sediment-water interface; Plate 2.3F). *Ophiomorpha annulata* is a common interface trace fossil found along thin-bedded turbidites in this ichnofabric. The palaeoenvironment is inferred to be relatively quiescent compared with other parts of the basin. Accessory trace fossils include rare ?*Asterosoma radiciforme* with *Scolicia prisca* which is found in high density patches. This low ichnological abundance may be attributed to the patchy nature of endobenthic communities (cf. McIlroy, 2007). This ichnofabric indicates a community of largely vagile deposit feeding organisms probably dominated by echinoids, crustaceans, and worms.

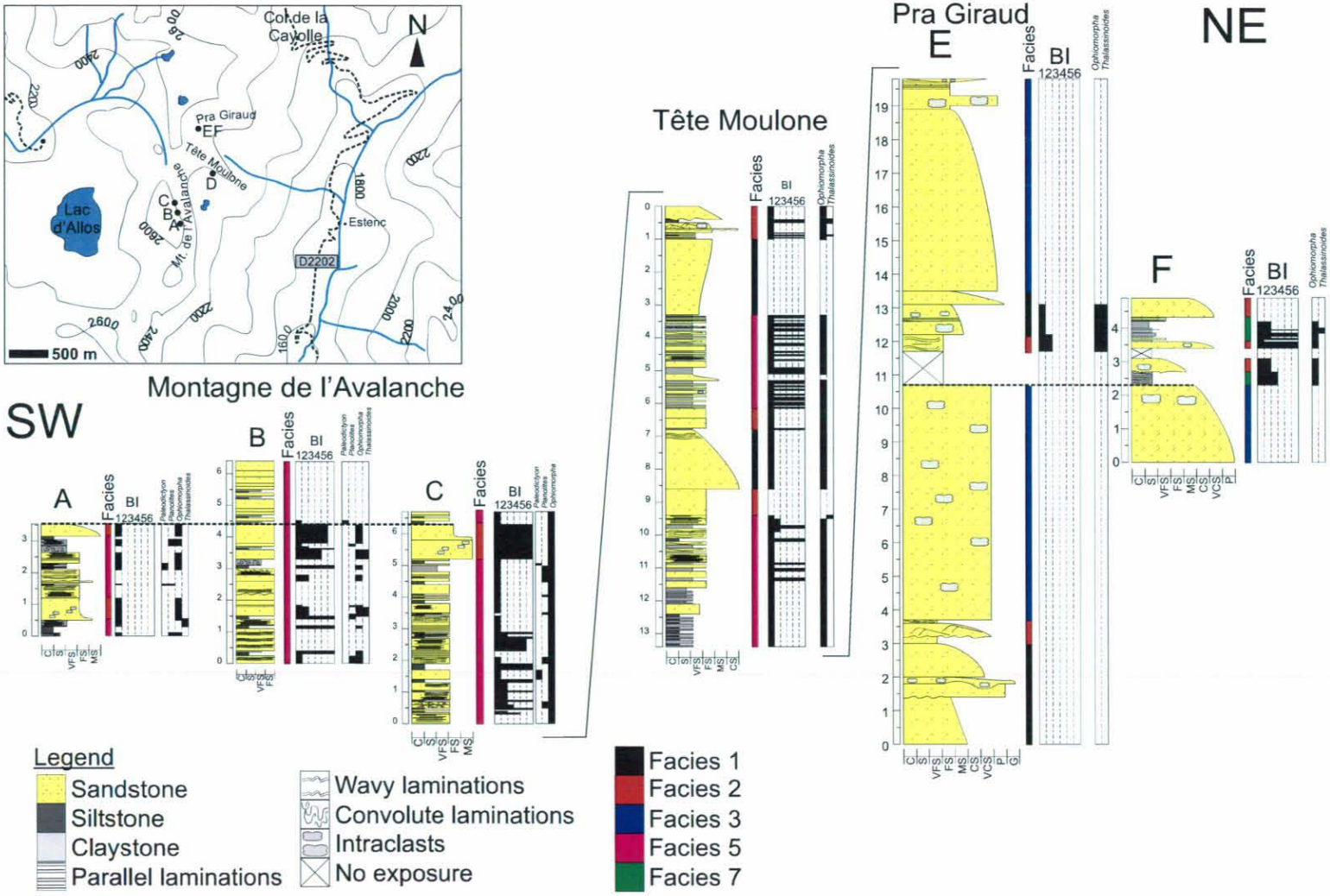
2.7. Ichnological interpretation of depositional environments in the Grès d'Annot Basin

2.7.1. Basin floor settings

2.7.1.1. Channel environments

The sedimentary succession of the Col de la Cayolle area is shown in Fig 2.4. The stratigraphy includes thick-bedded, coarse-grained, and sand-rich turbidites (exposed to the northeast) replaced upwards by a heterolithic succession of very fine sandstone, siltstone, and claystone (exposed to the southwest; Fig. 2.4). The lower part of the succession exposes thick-bedded, 1–4 m, coarse- to medium-grained, amalgamated sandstones associated with facies 1 and 3 (Figs 2.4–2.5A, C). The basal sandstones thicken and coarsen upwards in metre scale packages that contain little or no interbedded mudstone. These thick-bedded packages are interpreted as channel sands deposited from high volume turbidity currents. Massive sandstones are upwardly replaced by thin- to medium-bedded sandstones and an interbedded succession of very fine sandstone, siltstone, and claystone (Fig. 2.5A-B). These beds are interpreted to be channel-fill deposits filling a topographic low from low volume turbidity currents.

Ophiomorpha is abundant in both the thick-bedded and thin-bedded facies despite the change in hydrodynamic regime. Thick and massive sandstones are devoid of trace fossils except for the occasional *Ophiomorpha rudis*. In this case, the tracemakers were probably opportunistic animals, repopulating the environment during inter-turbidity current periods, or possibly transported in the most buoyant part of the flow (Grimm &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B
C
Facies
BI
123456
Tête Moulone
Pra Giraud
E
F
NE
Ophiomorpha
Thalassinoides
Legend
Sandstone
Siltstone
Claystone
Parallel laminations
Wavy laminations
Convolute laminations
Intraclasts
No exposure
Facies 1
Facies 2
Facies 3
Facies 5
Facies 7

Föllmi, 1994), then taking advantage of the newly oxygenated seafloor. There is no evidence of escape traces or colonization from below as documented by the multilayer colonizers of Uchman (1995b).

The thick-bedded and coarse-grained sandstone turbidites of the Col de la Cayolle area exhibit the *Ophiomorpha rudis* ichnofabric and the rare *Ophiomorpha rudis-Ophiomorpha ?nodosa* ichnofabric which is characteristic of this depositional setting. The low diversity ichnological suite of low abundance, post-depositional *Ophiomorpha* emphasizes the palaeobiological stresses present. These stresses probably included low nutrient levels in the clean organic-poor turbidite sandstones as well as high current energies. Other workers have found similar patterns of low diversity in channelized facies (Crimes *et al.* 1981; Uchman, 2001; Heard & Pickering, 2008).

The heterolithic sandstone and mudstone turbidites related to channel fill are also burrowed by *O. rudis*. The resultant ichnofabric contains other trace fossils indicating gradually ameliorating palaeoenvironmental conditions with deposition of more organic carbon-rich, fine-grained sediment. Ichnogenera include *Chondrites*, *Ophiomorpha*, *Paleodictyon*, *Phycosiphon*, *Planolites*, *Thalassinoides*, and *Zoophycos*. Apart from *Paleodictyon*, these trace fossils preserve deposit feeding communities, where *Ophiomorpha annulata*, *Ophiomorpha rudis*, and *Planolites* represent the activity of bulk sediment processors searching for organic-rich material. This higher ichnological diversity suggests the establishment of an equilibrium community. Low density turbidity currents, with low erosive power, increase the preservation potential of shallow tier trace fossils (Orr, 1994).

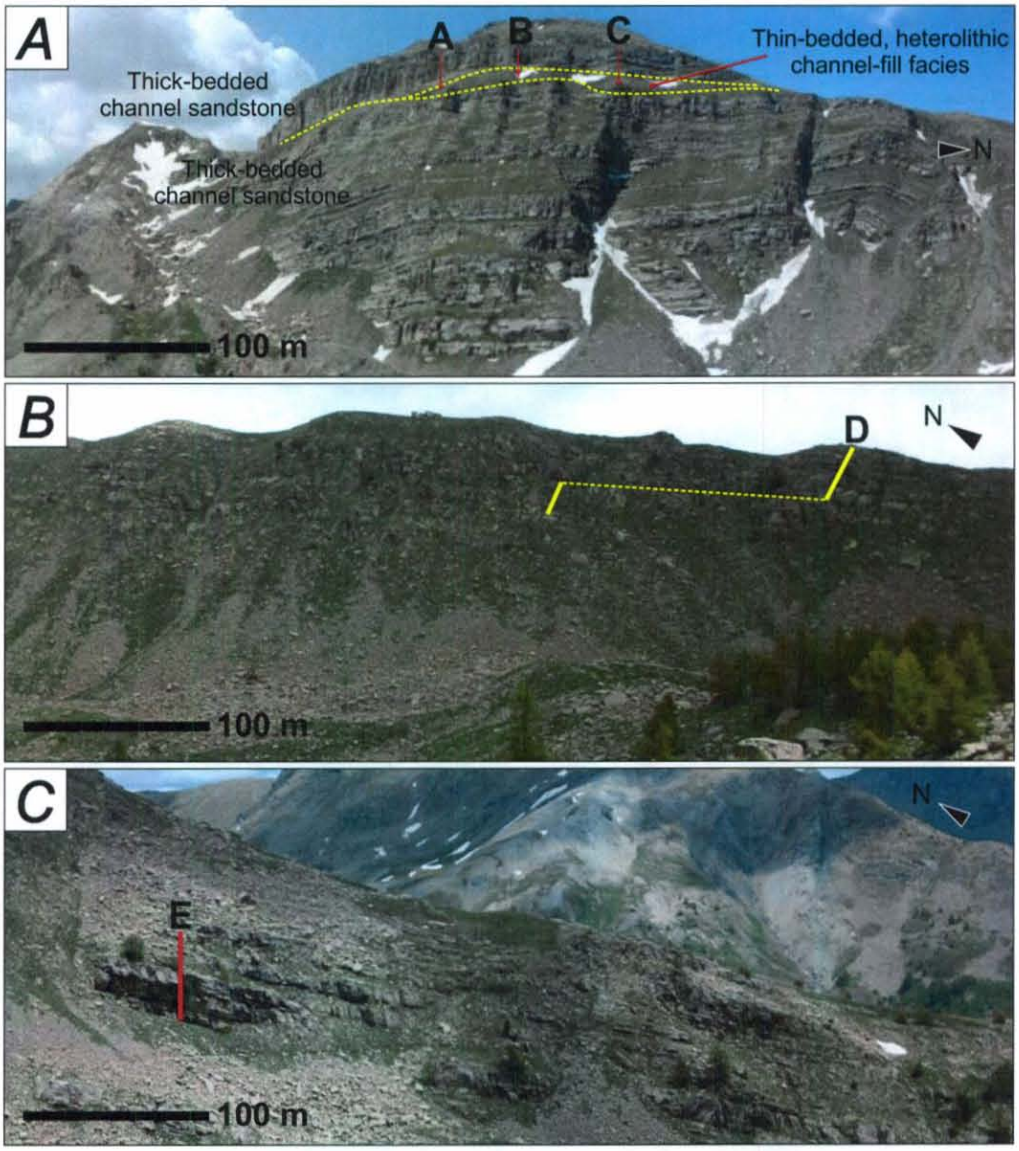

Fig. 2.5. Field images of the logged sections shown on Fig. 2.4. **A.** Montagne de l'Avalanche: channel sands (thickening- and coarsening-upward packages of sandstone turbidites; facies 1 and 3) dominate the lower stratigraphy with thin-bedded fine-grained, heterolithic succession of sandstones, siltstones, and mudstones filling a topographic low (channel fill facies; facies 5). **B.** Tête Moulone: thin-bedded facies with interbedded sandstones and mudstones, interpreted as lateral equivalents of the channel fill facies (facies 5) shown in B. **C.** Pra Giraud: thick-bedded and coarse-grained sandstone turbidites (facies 1 and 3) interpreted as a lateral equivalent of the channel sands in A.

7.1.2. Proximal fan environment

The Baisse de l'Aiguille outcrop consists of fining upward successions of thick- and medium-bedded sands with interbedded medium- to thin-bedded mudstones (Figs 2.6–2.7). Bed thicknesses are variable and the sandstone to mudstone ratios increasing upwards. The interpretation of this succession as a proximal fan is based on field observations of a sheet-like geometry for the sandstone beds, suggestive of deposition from unconfined flows (Fig. 2.6B; Uchman, 2001). Sedimentation rates associated with turbidity current events tend to be high in fan settings. This results from flow expansion as turbidity currents leave the confines of a channel (Pickering *et al.* 1989). The turbidity current becomes reduced in thickness and loses turbulence, causing rapid deposition.

The turbidite fan deposits contain very few trace fossils and little variability in ichnofabric. The *Ophiomorpha rudis* ichnofabric is characteristic with galleries of *O. rudis* being especially abundant in the finer grained, inter-turbidite mudstones. The only ichnological variability is the rare development of the *Ophiomorpha rudis-Thalassinoides suevicus* ichnofabric, which is documented from a limited number of inter-turbidite mudstone horizons. The burrows penetrate thick sandstone intervals (seen as vertical shafts), to exploit organic-rich inter-turbidite mudstones beneath. This behaviour implies a nutrient stress at the sediment-water interface with only deep-burrowing animals able to survive in this low nutrient setting.

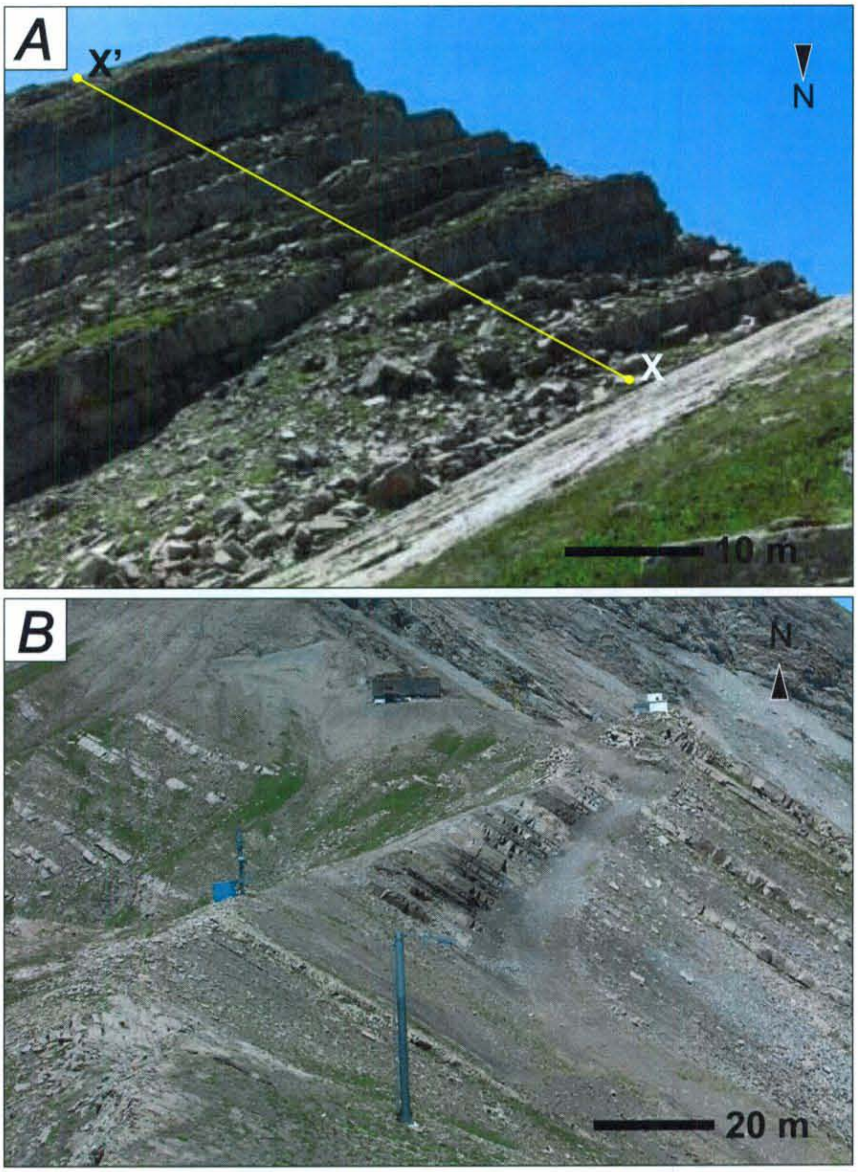

Fig. 2.6. Field images from the Baisse de l'Aiguille proximal fan deposit. **A.** The outcrop shows thick- and medium-bedded sandstone turbidites (facies 1) with a decrease in the sand:mud ratio up section (see Fig. 2.7). The graphic log presented in Fig. 2.7. is drawn along the line XX'. **B.** Thick packages of medium- to thick-bedded sandstone turbidites (facies 1) with interbedded thin- to medium-bedded mudstones (facies 7). The proximal fan deposits have a continuous, sheet-like geometry. The proximal fan deposits have a low ichnodiversity and abundance of trace fossils, dominated by *Ophiomorpha rudis* (see test and Fig. 2.7).

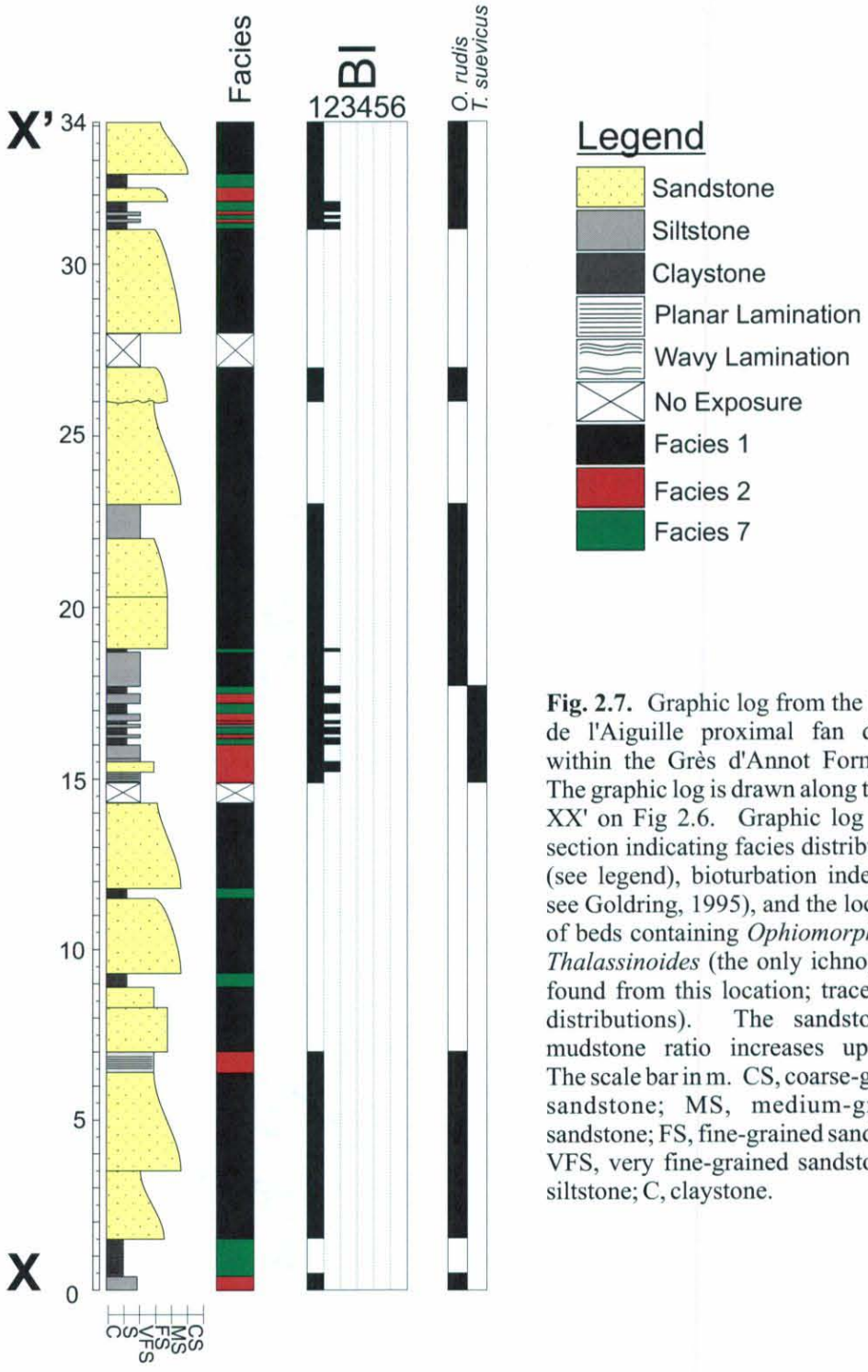

Fig. 2.7. Graphic log from the Baisse de l'Aiguille proximal fan deposit within the Grès d'Annot Formation. The graphic log is drawn along the line XX' on Fig 2.6. Graphic log of the section indicating facies distributions, (see legend), bioturbation index (BI; see Goldring, 1995), and the locations of beds containing *Ophiomorpha* and *Thalassinoides* (the only ichnogenera found from this location; trace fossil distributions). The sandstone to mudstone ratio increases upwards. The scale bar in m. CS, coarse-grained sandstone; MS, medium-grained sandstone; FS, fine-grained sandstone; VFS, very fine-grained sandstone; S, siltstone; C, claystone.

2.7.2. Ichnology of confining basin slope settings

Confining basin slope settings are those areas along a basin margin or inter-basin relief which influence the flow of turbidity currents, resulting in deposition (Kneller & McCaffrey, 1999, 2003). Confining basin floor settings studied include Montagne de Chalufy and the Braux locality (Fig. 2.1). The complex arrangement of sub-basins and intra-basin structural features in the Grès d'Annot Basin influenced the style of deposition of incoming turbidity currents (Sinclair & Tomasso, 2002). Through time, the confining basin slopes were progressively draped and locally onlappped by the hemipelagic Marnes Bleues Formation. This Formation was in turn buried by the Marnes Brunes Inférieures Formation which is the lateral and distal equivalent of the Grès d'Annot Formation (Figs 2.8–2.9). This stratigraphic succession is accompanied by an increase in sedimentation rate and bed thickness up section. The change in formation and facies is also associated with a change in the trace fossil assemblage and ichnofabric.

A diverse and abundant trace fossil assemblage was recorded from the interbedded successions of the Marnes Brunes Inférieures Formation. A nutrient-rich palaeoenvironment with no significant biological stresses is demonstrated by a diverse ichnofaunal assemblage. Preservation potential of shallow tier trace fossils (e.g. *Phycosiphon*) was enhanced by deposition of beds with low erosive power. An ichnological assemblage inferred to represent the activity of mobile and sessile deposit feeders is preserved. The relatively quiescent palaeoenvironment of the Marnes Brunes Inférieures Formation is dominated by the *Phycosiphon-Ophiomorpha rudis* ichnofabric.

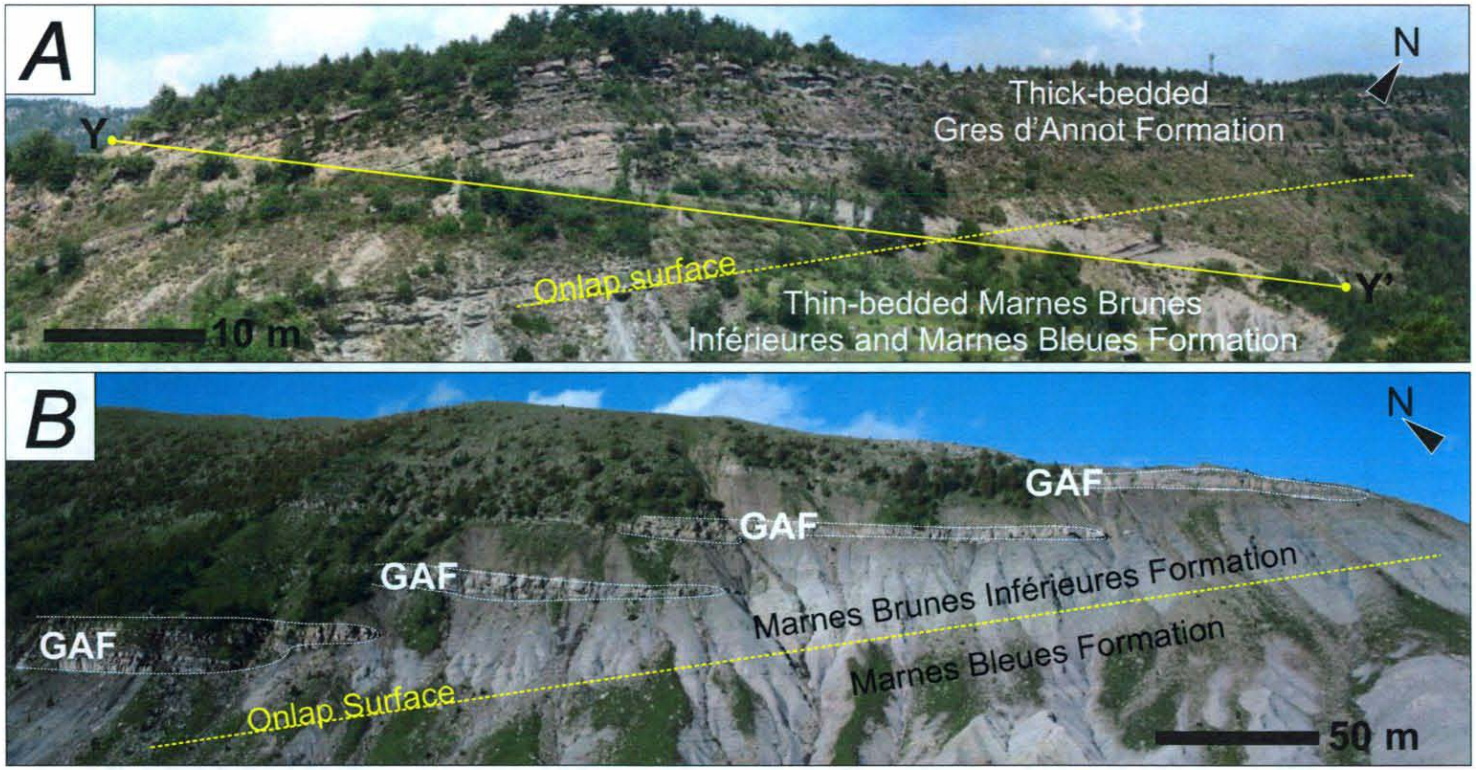

Fig. 2.8. Field images of confining basin slope settings. **A.** The Braux outcrop along the D110 road. Hemipelagic marlstones (Marnes Bleues Formation; facies 8) with interbedded thin-bedded turbidites (Marnes Brunes Inférieures Formation; facies 6) change to thick-bedded, coarse-grained sandstone turbidites (Grès d'Annot Formation; facies 1 and 4). YY' is the line of section for the graphic log on Fig. 2.9. **B.** The Montagne de Chalufy onlap section. Thick-bedded turbidites of the Grès d'Annot Formation (GAF, facies 1; highlighted) punctuate thin-bedded lateral and distal equivalents (i.e. the Marnes Brunes Inférieures Formation). Both formations onlap and pinch out onto the Marnes Bleues Formation on the ancient palaeo-slope.

This ichnofabric includes ?*Asterosoma*, *Ophiomorpha rudis*, *O. annulata*, *Phycosiphon*, *Planolites*, and *Scolicia*.

A dramatic change in the sedimentological and ichnological character of the successions comes with the deposition of the thick-bedded turbidites of the Grès d'Annot Formation. The onset of thick-bedded turbidite deposition marks a change to the *Ophiomorpha rudis* ichnofabric with some *O. rudis* penetrating turbidite sandstone beds up to 2 m thick (Plate 2.3F). These thick sandstone turbidites with their inter-turbidite mudstone and mudstone intraclasts contain *O. rudis* as their only trace fossil component. The *Ophiomorpha rudis-Ophiomorpha annulata* ichnofabric is observed in areas where the start of Grès d'Annot Formation deposition is marked by thin- to medium-bedded turbidites of facies 2. In most cases, however, the *Phycosiphon-Ophiomorpha rudis* ichnofabric changes abruptly to the *Ophiomorpha rudis* ichnofabric. Thick sandstone beds of facies 1 (Grès d'Annot Formation) are deposited on top of thin-bedded turbidites of facies 6 (Marnes Brunes Inférieures Formation; Fig. 2.9). There is a concomitant change to the *Ophiomorpha rudis* ichnofabric from the *Phycosiphon-Ophiomorpha rudis* ichnofabric with this change in depositional conditions and facies. The shift in ichnological assemblage indicates that the near-surface deposit feeding community was replaced by organisms which were forced to burrow to deeper levels in the sediment to find nutrition.

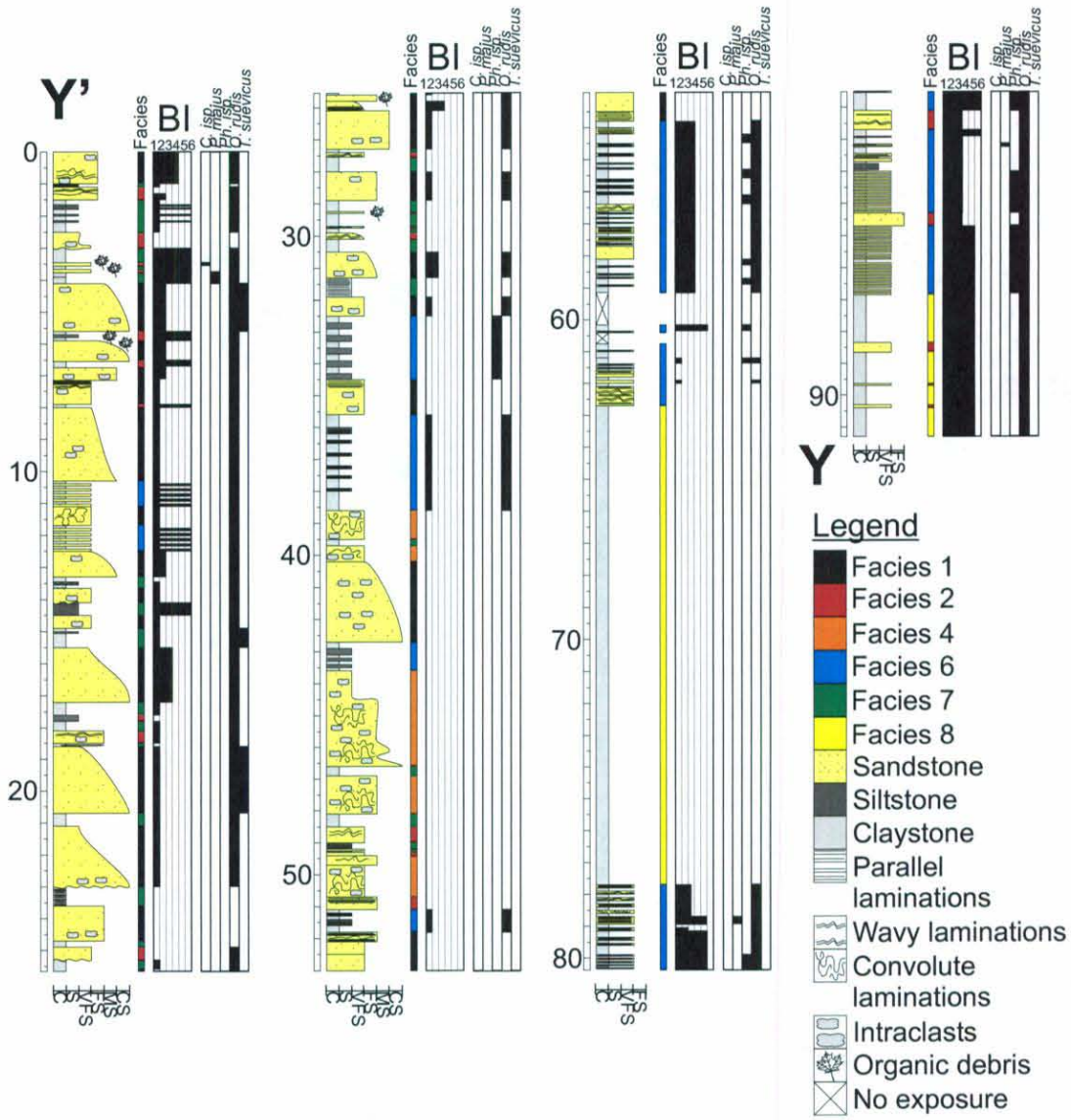

Fig. 2.9. The graphic log from the labelled points YY' on Fig. 2.8A showing fine-grained hemipelagic claystone (Marnes Bleues Formation) being punctuated by thin-bedded turbidites (Marnes Brunes Inférieures Formation) and then onlapped by the deposition of thick-bedded sandstone turbidites and debrites (Grès d'Annot Formation). The bioturbation index (BI) is displayed alongside the log and the ichnogenera present at stratigraphic intervals. *Ophiomorpha rudis* is the most abundance trace fossil recorded from the sandstone turbidites (facies 1) with *Phycosiphon* and *O. rudis* common in this the thin-bedded heterolithic sandstone and mudstone intervals (facies 6). The scale bars are in m. CS, coarse-grained sandstone; MS, medium-grained sandstone; FS, fine-grained sandstone; VFS, very fine-grained sandstone; S, siltstone; C, claystone.

2.8. Conclusion

This paper described the ichnotaxa and ichnofabrics of the Grès d'Annot Basin for the first time and demonstrated that trace fossils and ichnofabrics can be used to indicate changes in depositional and palaeoenvironmental conditions in deep-water palaeoenvironments. The siliciclastic fill of the Grès d'Annot Basin is characterized by a high abundance, low diversity assemblage dominated by the trace fossil *Ophiomorpha rudis*. Channel sands and thick-bedded sandstone turbidites have a low diversity assemblage restricted to post-turbidite colonization of locally abundant *O. rudis*. The *Ophiomorpha rudis* ichnofabric is dominant in these settings. Vertical shafts of deep *O. rudis* branch into horizontal galleries at depth along turbidite/inter-turbidite interfaces where the organism is inferred to have been deposit feeding. This is inferred by intensely bioturbated post-turbidite hemipelagites, perhaps due to high organic matter contents. *O. rudis* has been recorded penetrating turbidite sandstones >2 m thick (Plate 2.3F). Ichnofabric stacking patterns are interpreted to reflect fluctuations in nutrient availability and turbidity current energy.

Decreased volume, frequency, and erosive power of turbidity current events increase the preservation potential of shallow tier, pre-turbidite trace fossils. The diversity and complexity of ichnofabrics is amplified in these situations. Thin-bedded channel-fill and thin-bedded turbidites on confining basin slopes are characterized by episodic low volume turbidity currents. Such environments are dominated by the trace fossils of vagile, deposit feeding communities represented by the *Phycosiphon-*

Ophiomorpha rudis and *Ophiomorpha annulata-Planolites* ichnofabrics. These ichnofabrics have an ichnofauna that includes *Paleodictyon*, *Phycosiphon*, *Planolites*, as well as *Ophiomorpha annulata*, and *O. rudis* with rare and patchy occurrences of ?*Asterosoma*, *Chondrites*, *Scolicia*, and *Zoophycos*.

Shallow to mid tier trace fossils are uncommon and are found and restricted to thin-bedded facies probably as a result of non-preservation in high current energy settings. Some common deep marine ichnotaxa are poorly represented (e.g., *Chondrites* and *Zoophycos*) and other (largely interface) trace fossils characteristic of many ancient deep water systems (e.g. graphoglyptids; Seilacher, 1977) are absent. A sampling bias could account for a percentage of this imbalance (see McIlroy, 2004a, 2007) but could be attributed to low preservation potential due to the frequent occurrence of high volume, strongly erosional turbidity currents. Classic models of turbidite ichnology (e.g. Crimes, 1977; Uchman, 1995a, 1998) have been based on the richest ichnological successions and are probably, in themselves, not entirely representative of most turbidite settings. The confined nature of the Grès d'Annot Basin may also have contributed to low ichnodiversity through ponding of large volumes of sediment and concomitant suppression of the development of distal, thin-bedded facies. In combination, turbidity current energy, nutrient stress, and basin structure may have been the most significant controls on trace fossil assemblages documented herein from the Grès d'Annot Basin.

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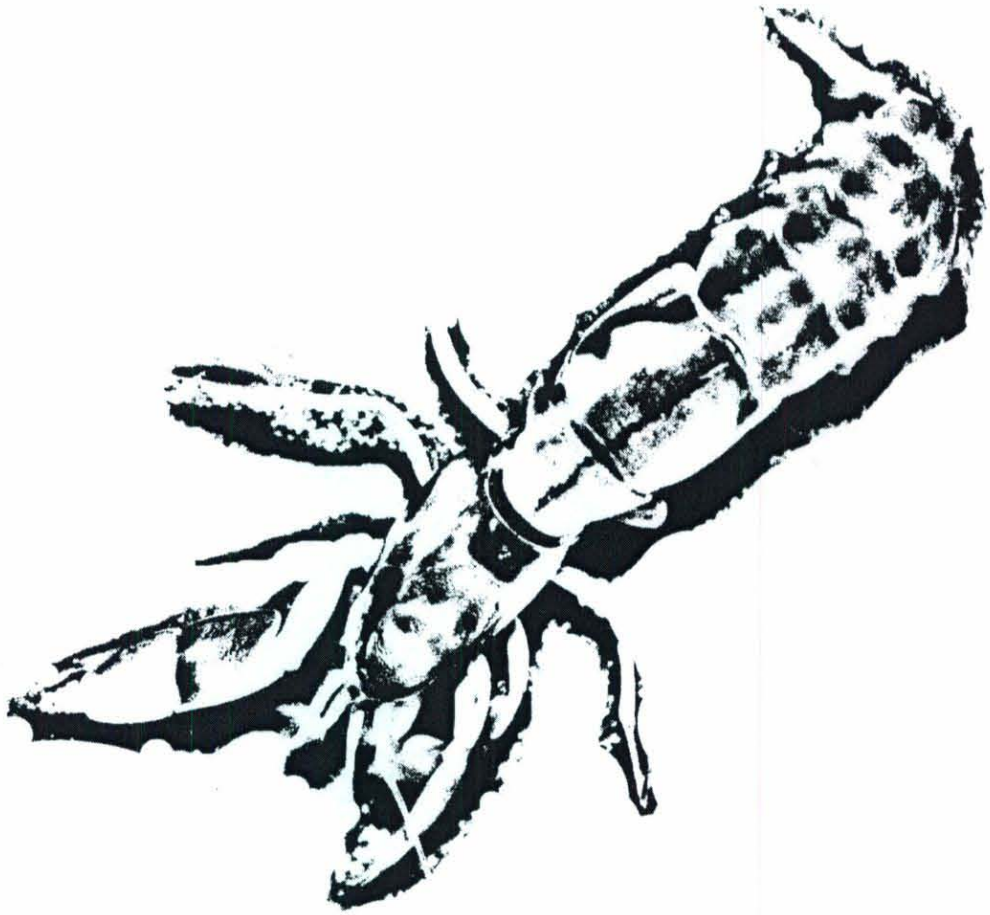
CHAPTER 3

Mining buried redox interfaces: an endobenthic feeding strategy in marine sediments



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CHAPTER 3

Mining buried redox interfaces: an endobenthic feeding strategy in marine sediments

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Abstract

The juxtaposition of buried oxygenated pore waters and organic carbon-rich, fine-grained sediment in turbidite systems presents a food resource for vagile endofauna. Numerous studies on the distribution of trace fossils in turbidite systems have recorded high abundances and densities of ichnogenera at sandstone-mudstone interfaces. This paper provides a possible explanation for the observed preference for burrowing along lithological contacts which has hitherto been unexplained. Sand-mud interfaces provide ideal opportunities for micro- and macro-organisms to feed and respire in the sediment. Based on field observations, laboratory mesocosm experiments, and theoretical considerations it is here suggested that the interface between deep-buried sand and mud is a zone of high microbial activity and productivity for both aerobic and anaerobic microbes, which attract deep-burrowing endobenthic organisms to this food resource. Deep-tier interface trace fossils like *Ophiomorpha* and *Thalassinoides* are interpreted to

be the burrows of deposit feeding organisms that fed on: (1) detrital organic matter in fine-grained sediment; (2) microbes (possibly cultivated) that exploit geochemical gradients between well-oxygenated sand and organic matter found in mud; and (3) dissolved organic carbon produced by microbial metabolism in these zones of enhanced productivity. Using modern *Ophiomorpha* tracemakers we combine mesocosm experiments, CT image analysis, and geochemical data to explain our field observations that deep burrowing organisms commonly exploit sand-mud interfaces in turbidite systems.

3.1. Introduction

Trace fossils from deep marine turbidite palaeoenvironments are commonly preserved at sandstone-mudstone interfaces with post-depositional trace fossils like *Ophiomorpha* and *Thalassinoides* common in post-Mesozoic turbidite systems (Chapter 2; Seilacher, 1962; Uchman, 1995, 1998, 2009; Heard & Pickering, 2008; Phillips *et al.* 2011). Both ichnogenera are characterized by horizontal or sub-horizontal branching galleries at depth in the substrate connected to the sediment-water interface by vertical or oblique shafts which can be over 1 m long (Uchman, 2009). At depth these horizontal galleries commonly anastomose producing burrow networks that may be polygonal or irregular (Bromley, 1996; Uchman, 2009). Horizontal galleries are commonly constructed at sandstone-mudstone interfaces at the base of turbidites (Fig. 3.1A) or in buried hemipelagite (Fig. 3.1B; Uchman, 1995, 1998; Heard & Pickering, 2008; Phillips *et al.*

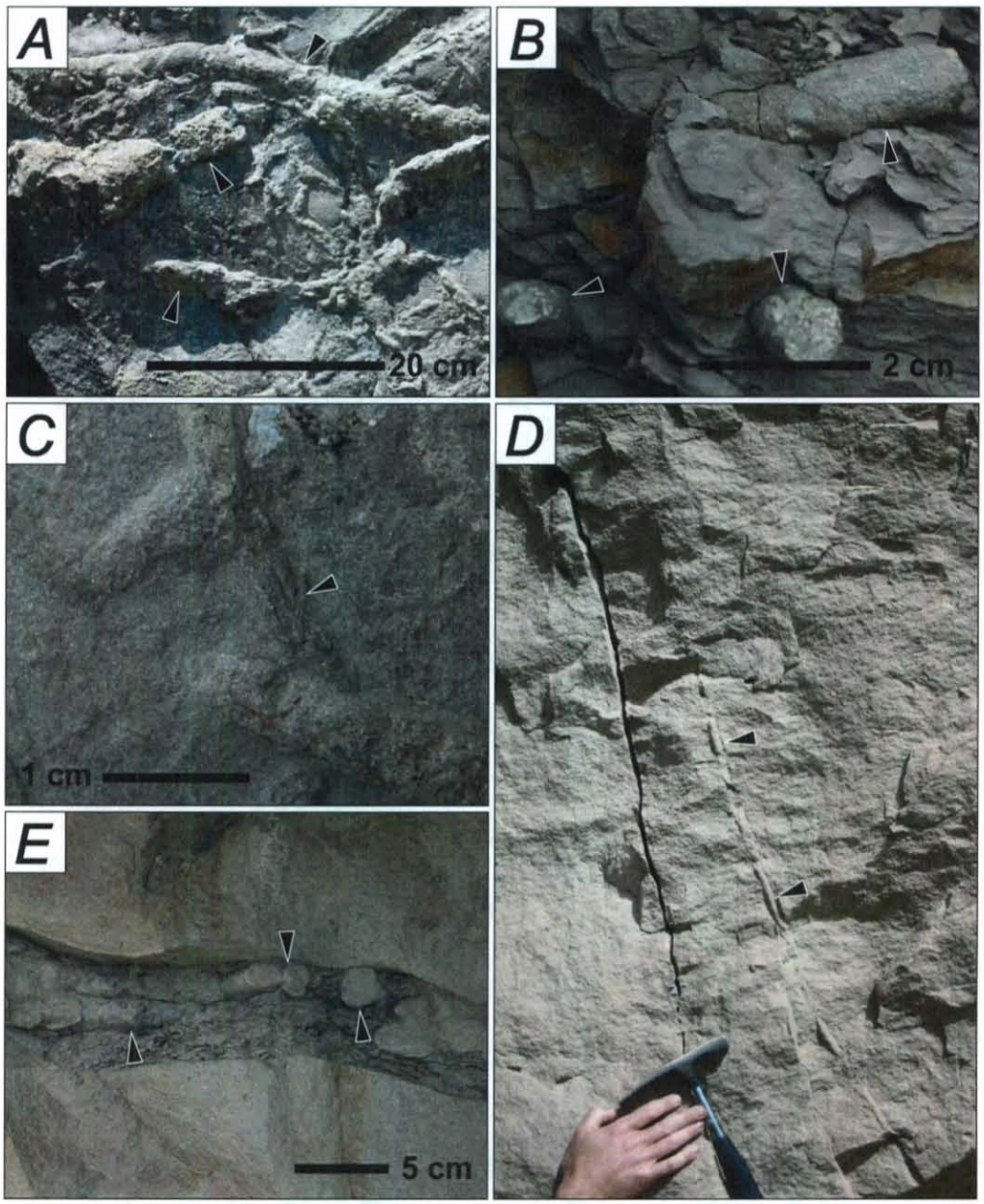


Fig. 3.1. Field images showing trace fossil distribution in an ancient turbidite system, the Eocene/Oligocene Grès d'Annot Formation, SE France. **A.** Numerous horizontal and pellet-walled *Ophiomorpha* on the sole of a sandstone turbidite (examples arrowed). **B.** *Ophiomorpha rudis* galleries (arrowed) in an inter-turbidite mudstone . **C.** *Thalassinoides* with bioglyphs (arrowed) in a sandstone turbidite (indicating firm substrate). **D.** >2 m long *Ophiomorpha* burrow through a sandstone turbidite. Hammer for scale. **E.** Mudstone intraclast in a sandstone turbidite intensely mined by *Ophiomorpha rudis* (arrowed).

2011). *Ophiomorpha* and *Thalassinoides* are similar in gross morphology but the *Ophiomorpha* wall is lined, at least partially, by small packets of usually fine-grained sediment termed pellets (Frey *et al.* 1978). In contrast, *Thalassinoides* is unlined and when excavated in a firm substrate the burrow wall may be ornamented with scratch marks (bioglyphs) produced during burrow excavation (Fig. 3.1C; Frey *et al.* 1978).

Ophiomorpha is seen in high abundance, and often mono-ichnogeneric, assemblages in thick-bedded turbidites in the Eocene/Oligocene Grès d'Annot Formation, SE France (Chapter 2; Phillips *et al.* 2011). The most common taphonomic expression of *Ophiomorpha* in the Grès d'Annot Formation is in convex hyporelief at sandstone-mudstone interfaces (e.g. as interface trace fossils; Fig 3.1A). These interfaces are commonly found to be highly bioturbated with numerous generations of burrows seen cross-cutting each other (Fig. 3.1A). We have also observed that large mudstone intraclasts incorporated into base of slope turbidites are bioturbated by *Ophiomorpha* (Fig. 3.1E). The intensity of bioturbation of the intraclasts (80-90%) is high relative to the surrounding sandstone suggesting that the mud clasts, and by extension the pre-turbidite mud, were a valuable resource for the *Ophiomorpha* and *Thalassinoides* tracemakers. The inferred behaviour is deposit feeding. The abundance of trace fossils (particularly *Ophiomorpha*) at sandstone-mudstone interfaces and within mudstone intraclasts in the Grès d'Annot turbidite system suggests that the deep-burrowing progenitors sought out sand-mud interfaces deep in the sediment. Further field observations have indicated that sandstone-sandstone interfaces in turbidite successions (i.e. surfaces of amalgamation) can provide insight into *Ophiomorpha*-producer behaviour. *Ophiomorpha* can be seen in a sandstone bed above a surface of

amalgamation, but is absent below it (Fig. 3.2). This provides an important insight regarding the feeding strategy of the *Ophiomorpha*-forming organism (discussed below).

This paper poses the question: why did the *Ophiomorpha* and *Thalassinoides* tracemakers burrow through thick sandstone beds to produce extensive horizontal galleries at underlying sand-mud interfaces? What are the possible feeding strategies of deep-burrowing organisms in turbidites settings? The distribution of *Ophiomorpha* and *Thalassinoides* were studied in a siliciclastic system in the field (the Grès d'Annot Basin; Chapter 2; Phillips *et al.* 2011). The distribution of modern *Ophiomorpha* and *Thalassinoides* tracemakers were studied in mesocosm laboratory experiments to elucidate the behaviour of deep-burrowing organisms at sand-mud interfaces. Burrow distribution and tracemaker behaviour are examined through mesocosm tank experiments and CT imagery and are considered in a biogeochemical context. The effects of bioturbating and bioirrigating organisms on the organic carbon content (TOC) and carbon isotope fractionation ($\delta^{13}C_{org}$) of the host sediment were measured to investigate how burrowing animals altered the sediment geochemistry and if this can be attributed to tracemaker behaviour. This paper aims to provide a behavioural model for the distribution of interface trace fossils in ancient turbidite settings.

3.2. Marine sediment geochemistry

Modern marine sediments are predominantly a reducing environment capped by a thin oxic surface layer in contact with oxygenated bottom waters (Kristensen, 2000). The

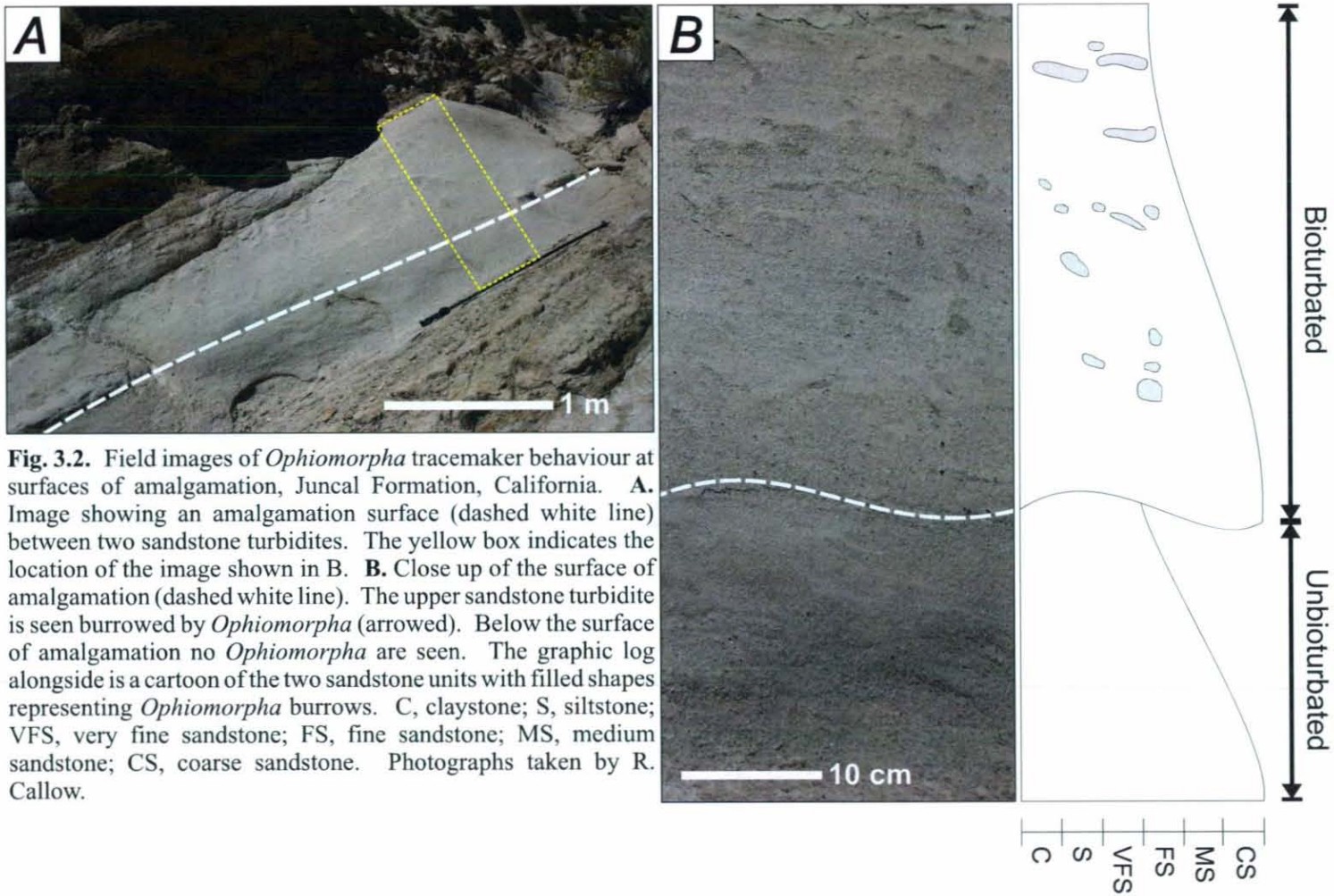


Fig. 3.2. Field images of *Ophiomorpha* tracemaker behaviour at surfaces of amalgamation, Juncal Formation, California. **A.** Image showing an amalgamation surface (dashed white line) between two sandstone turbidites. The yellow box indicates the location of the image shown in B. **B.** Close up of the surface of amalgamation (dashed white line). The upper sandstone turbidite is seen burrowed by *Ophiomorpha* (arrowed). Below the surface of amalgamation no *Ophiomorpha* are seen. The graphic log alongside is a cartoon of the two sandstone units with filled shapes representing *Ophiomorpha* burrows. C, claystone; S, siltstone; VFS, very fine sandstone; FS, fine sandstone; MS, medium sandstone; CS, coarse sandstone. Photographs taken by R. Callow.

depth of oxygen penetration, by molecular diffusion, is on the order of millimetres where surface sediment has a high respiratory activity (Reimers *et al.* 1984). This penetration depth is increased by benthic animals mixing the sediment resulting in a thicker oxygenated surface layer. The bioturbated layer is typically c. 6 cm thick in modern deep-sea sediments under steady-state conditions (Teal *et al.* 2008). Non-steady state conditions such as those influenced by turbidite deposition can change environmental conditions on the ocean floor (Wilson *et al.* 1986; Buckley & Cranston, 1988). Turbidity currents may deliver oxygen-enriched waters (Sholkovitz & Soutar, 1975) and rapidly deposit thick layers of sediment which are likely to be well-oxygenated as oxygen is entrained during turbidity current flow (Wetzel & Uchman, 2001). Consequently, turbidity currents can deposit thick layers of oxygenated sediment suppressing the depth of the redox boundary in the sediment (Wilson *et al.* 1986). Sediment oxygenation is short-lived as free oxygen is used by microbial processes causing the redox front to rise through the turbidite back to its near-surface position (Colley *et al.* 1984; Thomson *et al.* 1984; Wilson *et al.* 1986). Numerous studies have described the movement of the redox boundary in response to turbidite deposition but they have not examined its rate of return to its near-surface position (Colley *et al.* 1984; Thomson *et al.* 1984; Wilson *et al.* 1986). This, as yet, has not been quantified in the literature. Despite the inevitable rise of the redox boundary, deep-sediment oxygenation can be locally maintained by bioirrigation.

Bioirrigation is the pumping of water into, and out of, a burrow by biologically induced currents generated by the burrow inhabitant (Gust & Harrison, 1981; Herringshaw *et al.* 2010). Burrow ventilation delivers oxygenated water (and possibly nutrition for suspension feeders) to the burrower and allows oxygen to penetrate the

sediment to greater depths than can be achieved by molecular diffusion. Organisms that bioirrigate can live deeper in the sediment profile and are able to exploit deep-buried sources of organic carbon. As a result of bioirrigation, open burrows can be simplistically thought of as an extension of the sediment-water interface (Aller, 1982; Papaspyrou *et al.* 2006) increasing the sediment surface area in contact with oxygenated water and increasing the total oxygen flux into the sediment (Zorn *et al.* 2006). Free oxygen can diffuse into the sediment through the burrow wall resulting in a geochemical gradient that is, relative to the burrow surface, a three-dimensional extension of the seafloor (Fig. 3.3A; Aller, 1982).

Organic carbon in particulate organic matter (POM) is the most important electron-donor oxidized by microbial reactions within the sediment (Canfield, 1989, 1993, Coleman & Raiswell, 1993). POM is oxidized in a number of microbial pathways in geochemical zones that utilize different electron acceptor species (Table 3.1). These zones are stratified vertically away from the source of available oxygen, which can either be the seafloor or a burrow margin (Fig. 3.3; Aller, 1982; Sundby, 2006). This stratification is a result of micro-organisms utilizing available electron acceptors that give the highest yield of energy. The most energetically favourable electron acceptors per mole of oxidized carbon are utilized first, closest to the sediment-water interface, while less energetically favourable electron acceptors are used at increasing depths (Froehlich *et al.* 1979; Berner, 1980). The order of the principal electron acceptors follows a trend reflecting the Gibbs free energy yield for the reduction of each species (Table 3.1). Microbes that preferentially use oxygen as an electron acceptor in the metabolism of organic carbon have a competitive advantage in the oxic zone because oxygen provides

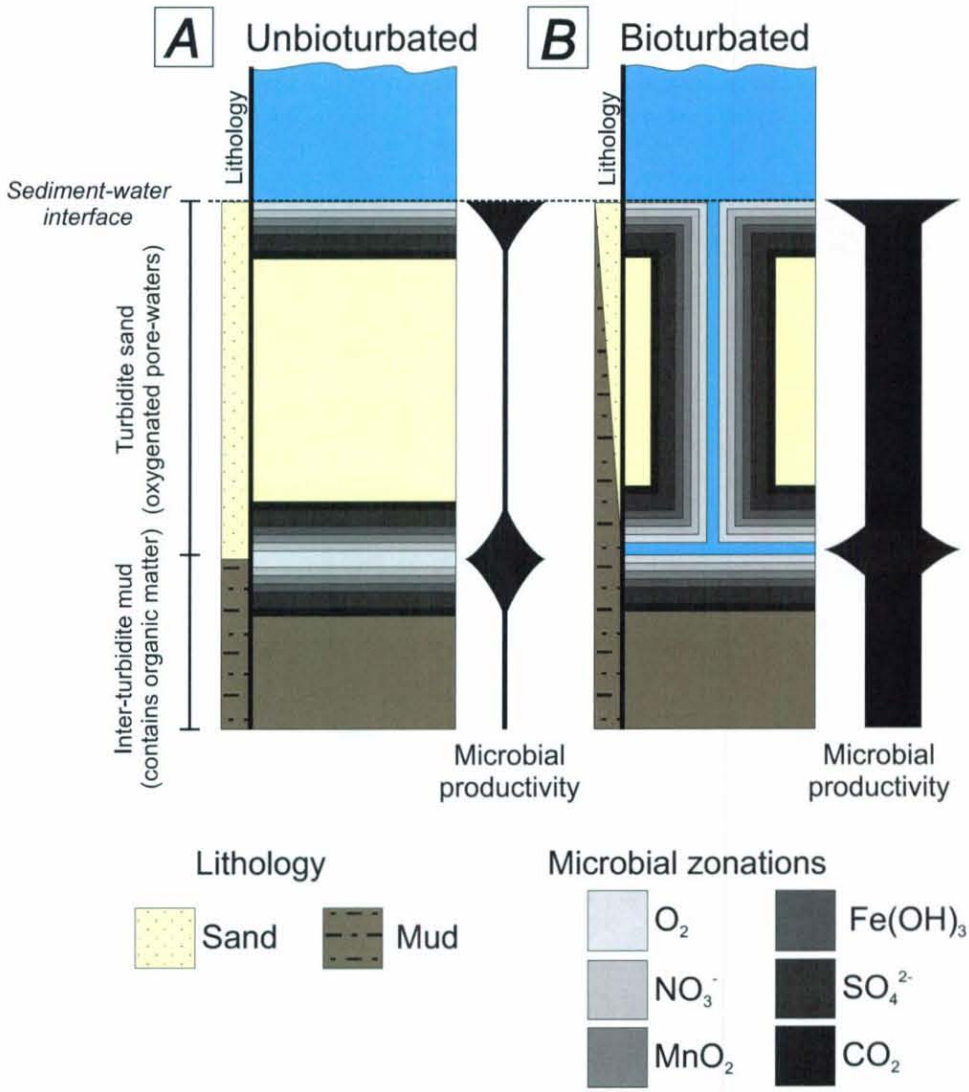


Fig. 3.3. Pump-priming of the sedimentary system for deep-sediment miners based on the model of Aller (1982). **A.** Turbidite sand deposited on top of an inter-turbidite organic-rich mud. No bioturbation. The sand is well-oxygenated after deposition but is an organic matter-limited microenvironment. The mud horizon produces an oxidant-limited microbial system as oxygen is used as zones of microbial productivity are found at the interface between the oxygenated sand and the organic-rich mud. The line alongside shows the increases and decreases in microbial productivity through the succession. **B.** A sand turbidite deposited on top of a muddy interbed with bioturbation an organism has burrowed through the sand to the sand-mud interface and burrowed horizontally at that horizon. Oxygen is pumped, continually or periodically, deep into the sediment by the tracemaker. Bioirrigation means that the oxygen flux into the sediment is increased resulting in a higher microbial productivity compared to unbioturbated strata. The short-lived geochemical gradients shown in Fig. 3.3A can be maintained through bioirrigation, allowing aerobic microbial colonization of the deep sediment.

Reaction	Free energy yield, ΔG° (KJ mol-1 of CH_2O)
Oxic respiration:	
$CH_2O + O_2 \rightarrow CO_2 + H_2O$	-475
Nitrate reduction:	
$5CH_2O + 4NO_3^- \rightarrow 2N_2 + 4H_2CO_3^- + CO_2 + 3H_2O$	-448
Manganese reduction:	
$CH_2O + 3CO_2 + H_2O + 2MnO_2 \rightarrow 2Mn^{2+} + 4HCO_3^-$	-349
Iron reduction:	
$CH_2O + 7CO_2 + 4Fe(OH)_3 \rightarrow 4Fe^{2+} + 8HCO_3^- + 3H_2O$	-114
Sulphate reduction:	
$2CH_2O + SO_4^{2-} \rightarrow H_2S + 2HCO_3^-$	-77
Methane production:	
$2CH_2O + 2H_2O \rightarrow CH_4 + CO_2$	-58

Table 3.1. Oxidation pathways and free energy yields of microbial reactions (taken from Berner, 1980).

the highest yield of energy per mole of carbon (Table 3.1; Glud *et al.* 1994). It must be noted, however, that not all microbes in the oxic zone will use oxygen as the terminal electron acceptor as anoxic microenvironments may be present, especially if the system is non-steady state (Froelich *et al.* 1979). When oxygen levels drop below a concentration sufficient for this reaction to be energetically favourable, either in microenvironments or in deeper oxygen-depleted zones, microbes that utilize the next most energy efficient electron acceptor will dominate the microbial community and contribute greatest to the oxidation of organic matter. The net effect of microbial decomposition in the sediment is the production of labile dissolved organic carbon (DOC) from refractory POM. The breakdown of POM is greatly enhanced by the surface-area to volume ratio of the detrital organic matter. POM can be broken down by: (1) physical sedimentary processes; (2) by the passive activities of burrowing organisms; (3) by active disaggregation during mastication and ingestion by benthic organisms, and (4) by the metabolic activities of anaerobic micro-organisms, sulphur-reducing bacteria in particular (Canfield, 1989).

3.3. Hypothesis: burial of organic-rich horizons

Fine-grained inter-turbidite and hemipelagic sediments may contain organic matter sourced from shallower depths offering a potential source of nutrition for benthic organisms. Rapid burial of inter-turbidite mud by oxygenated turbidite sand can isolate potentially organic carbon-rich horizons from the water column. The deep-burrowing progenitors of *Ophiomorpha* and *Thalassinoides* are here hypothesized to exploit these

buried horizons. Constructing and bioirrigating burrows along buried sand-mud interfaces produces a geochemical microenvironment suitable for habitation by endobenthic organisms. The presence of free oxygen within ventilated burrows leads to the development of zones of microbial remineralization (Aller, 1982). In this situation the redox gradients are reversed as oxygen is delivered to deep-buried sediments diffusing upwards through horizontal burrows along sand-mud interfaces (Fig. 3.3B).

Our model predicts that this biologically induced source of free oxygen encourages microbial productivity in the near-burrow environment, especially where mud pellets or mucus lines the burrow margin (i.e. where microbial concentrations and POC concentrations are likely to be high). We predict that the profusion of interface trace fossils observed in the Grès d'Annot Formation, and other turbidite systems, is a result of deep-burrowing organisms generating and maintaining geochemical gradients at sand-mud interfaces. It is here postulated that bioirrigation allows aerobic microbial reactions to occur deep in the sediment profile associated with oxygenated burrows. Further, we suggest that by culturing microbes within the burrow walls the inhabitant can produces a substantial DOC resource to meet or supplement its nutritional requirements at depth in the sediment. This is proposed as an otherwise unexploited niche which confers a unique advantage to deep-burrowing organisms like the progenitors of *Ophiomorpha* and *Thalassinoides* observed in the Grès d'Annot Formation (Chapter 2; Phillips *et al.* 2011). This model is tested below.

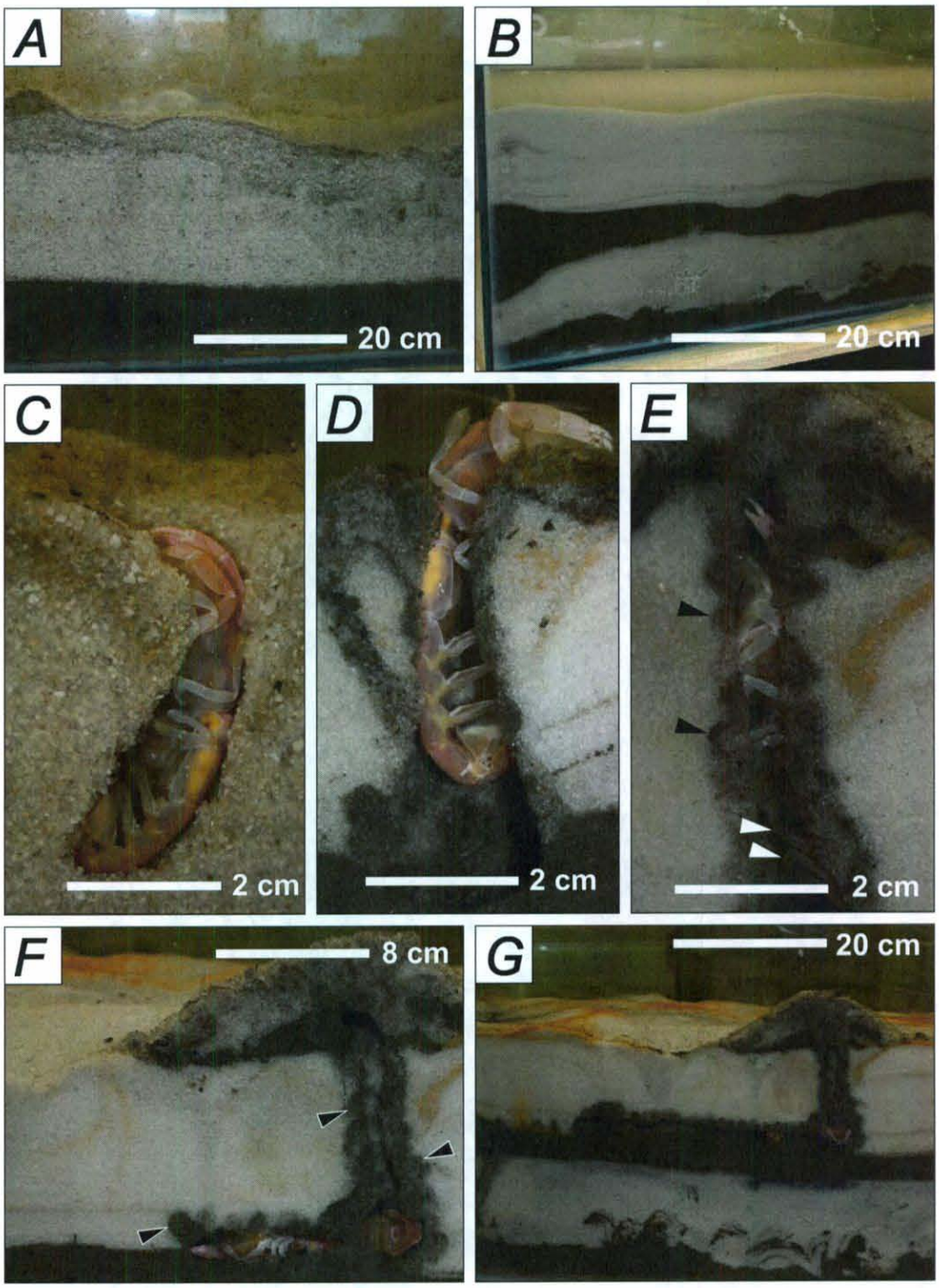
3.4. Methods

3.4.1. Experimental design

Two mesocosm experiments were constructed to simulate the vertical stratigraphy made by sand-rich event beds overlying natural fine-grained sediment (containing organic matter), analogous to a turbidite-hemipelagite succession (Plate 3.1). Mesocosms (measuring 75 cm long by 40 cm wide by 35 cm high) were fed by recirculating, chilled saltwater to provide an oxygenated marine water column at 14°C. Salinity was monitored and maintained at 34 ‰.

3.4.1.1. Tank 1 (Plate 3.1A)

Two-layer starting conditions. Mud-rich sediment [mean grain size = 17 μm, Standard Deviation (S.D.) = 29 μm] was added as a 5 cm thick basal layer. Organic matter within this fine-grained material was a potential food source for bioturbating organisms. Overlying the mud was well-sorted, coarse-grained, 99% quartz sand [mean grain size = 852 μm, Standard Deviation (S.D.) = 423 μm]. The sand layer material was bought builders sand (organic-poor). This set up was designed to simulate the sediment profile after a single turbidity current event, enabling assessment of whether burrowing organisms would burrow down through a bed of sand in order to find and mine an organic carbon-rich horizon below. This could then be assessed by examining the distribution of burrows through the sediment column.


A
20 cm
B
20 cm
C
2 cm
D
2 cm
E
2 cm
F
8 cm
G
20 cm

3.4.1.2. Tank 2 (Plate 3.1B)

This mesocosm contained alternating layers of sand and fine-grained material. Two 7 cm-thick layers of well-sorted, fine-grained, 99% quartz sand [mean grain size = 476 μm, Standard Deviation (S.D.) = 196 μm] were interlayered with mud-rich marine sediment [mean grain size = 70 μm, Standard Deviation (S.D.) = 69 μm], 3 cm thick. The fine-grained sediment was collected from an estuary near Fox Trap, Conception Bay South, Newfoundland. Again, the material for the sand layers was bought builders sand. The sediment profile of this tank was designed to simulate two thin event beds deposited by turbidity currents. The experiment was designed to test the idea that a bioturbating organism would burrow through multiple beds and ramify along multiple sand-mud interfaces, thereby maximizing its potential food sources. Both mesocosms were left to equilibrate for one week before tracemakers were introduced.

3.4.1.3. The tracemaker

Modern thalassinid crustaceans construct burrows that are morphologically similar to *Ophiomorpha* and *Thalassinoides* and are considered analogues for the ancient tracemakers (Weimer & Hoyt, 1964; Frey *et al.* 1978). The ghost shrimp *Neotrypaea californiensis* (formerly *Callianassa californiensis*; following Manning & Felder, 1991) was chosen for this experiment. *N. californiensis* is a well-studied; mostly deposit feeding, shallow-water species chosen because of the similarities between the morphology of its burrow and *Ophiomorpha* and *Thalassinoides* (Miller & Curran, 2001). *N. californiensis* is known from mudflats and tidal plains along the North American seaboard from Alaska to Mexico (MacGinitie, 1934) where it constructs deep galleries in

the sediment, 50-100 cm below the sediment-water interface (Miller, 1984). Specimens of *N. californiensis* were collected from the coast of Oregon, USA. Five tracemakers were introduced to each tank and left to acclimatize and burrow. A period of eight months followed where burrowing and feeding behaviours were observed. At the end of this time morphological and geochemical data were collected.

3.4.1.4. CT scanning

Mapping the distribution of burrows was achieved using Computed Axial Tomography (CT) scanning with a Toshiba Xpress/GX medical CT scanner at Memorial University. Tanks were placed on the patient gantry and scans made using a source radiation of 130 kV and an intensity of 200 mA. Transverse slices 1 mm thick were imaged every 10 mm. Each slice/image was image processed to highlight the open burrows. This stack of images was rendered volumetrically to produce a three-dimensional reconstruction of the burrow system using VolView 2.0 (Kitware Inc.).

3.4.1.5. Sampling

After CT scanning, the tanks were serially sliced to retrieve samples for geochemical data; total organic carbon (TOC) and stable isotope analysis ($\delta^{13}C_{org}$). Slices were excavated to the full depth of the tank in 3 cm increments. Photographs were taken to help understand burrow system distributions. Samples were taken for geochemical analysis from Tank 2, from bioturbated material (burrow linings and pellets) and non-bioturbated muds. Samples were crushed with a pestle and mortar to produce a fine powder. The powder was then heated at 40°C for several days to dry. Samples were then

added to vials of 10% HCl to dissolve any carbonate present. This process was repeated three times before the samples were washed with distilled water and maintained at 40°C for several days to dry. Geochemical analyses were carried out at the TERRA Facility at Memorial University. Prepared samples weighing 0.02–0.1 mg were placed into tin capsules and combusted at 1800°C. The liberated CO_2 was analysed using a Carlo Erba Elemental Analyser connected to a DeltaVPlus mass spectrometer. Total organic carbon values are measured in weight percent while stable isotope values ($\delta^{13}C_{org}$) are measured in parts per mil relative to the Pee Dee Belemnite standard (Coplen *et al.* 2006).

3.5. Observations and results

3.5.1. Behaviour and burrow distribution of Neotrypaea californiensis

Neotrypaea californiensis construct their burrows in stages. Initially the shrimp burrowed vertically from the sediment-water interface to a sand-mud interface (Plate 3.1D-E). At the sand-mud interface, *N. californiensis* burrowed horizontally above the mud layer. The shrimps used the mud to line the sides and roofs of their burrows producing a wall with a textured exterior, ornamented with mud pellets, and smoothed on the interior. These burrows (Plate 3.1F-G) are morphologically comparable to the trace fossil *Ophiomorpha rudis*; a burrow circular-to-oval in cross-section with a roof partially lined with oval or elongate muddy sand pellets, 2-4 mm in diameter (Uchman, 2009; Phillips *et al.* 2011). In our mesocosm experiments, *N. californiensis* lined the roof of its burrow

with pellets and partially lined the sides (cf. *O. rudis*; Plate 3.1F). Burrows were 10-15 mm in diameter. All the individuals of *N. californiensis* lined their burrows with either a thin, smooth mud lining (1 mm thick; Plate 3.1D) or the mud-pelleted wall (pellets 2 mm thick; Plate 3.1E-G), morphologically similar to ancient *O. rudis* (Uchman, 2009).

Observations made of burrows along the glass walls of the tanks showed that *Neotrypaea californiensis* preferentially constructed burrows along mud-sand interfaces (Plate 3.1F-G). Burrow morphologies elsewhere in the tanks were investigated using CT scanning. Three-dimensional reconstructions of these scans show that *N. californiensis* preferentially burrowed along sand-mud interfaces throughout the mesocosms (Fig. 3.4). Visual observation and CT images analysis has revealed that our shrimp burrow along sand-mud interfaces in both of the mesocosms (Plate 3.1; Fig. 3.4).

After burrows were constructed *Neotrypaea californiensis* was observed engaging in two principle behaviours: bioirrigating and feeding. The shrimps were seen bioirrigating for the vast majority of time. This involved the organisms positioning themselves in the vertical shafts of their burrows (close to the sediment-water interface) and beating their pleopods (back three appendages, or swimmerets) ventilated their burrows (Plate 3.1E). We observed *N. californiensis* periodically destroying, partially ingesting, and reforming the wall pellets which could suggest that there was possibly some nutritional value in the mud-rich pellets (Plate 3.1F).

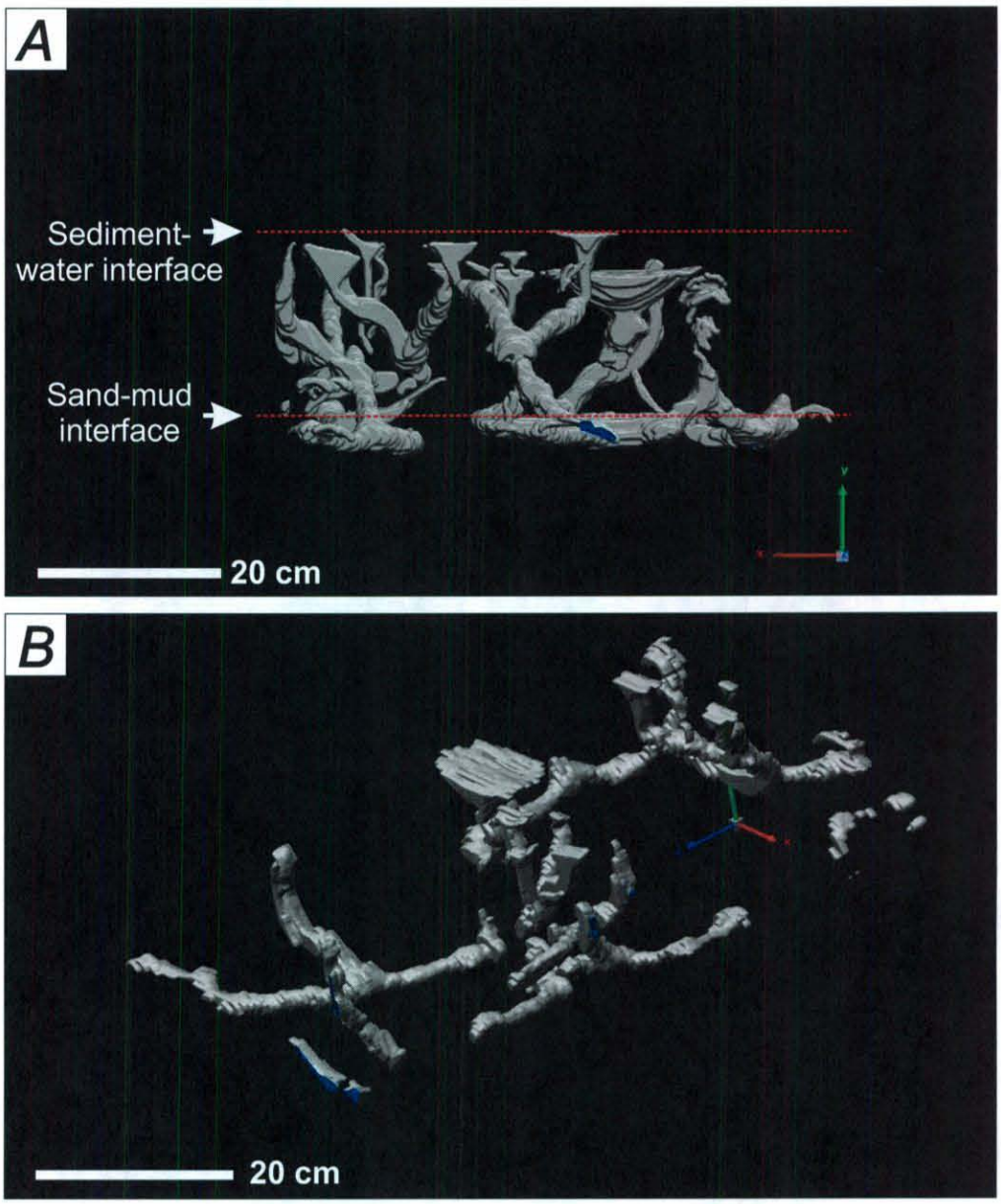


Fig. 3.4. Three-dimensional burrow reconstructions from Tank 1 (Plate 3.1A). **A.** Numerous vertical shafts ramifying to horizontal tunnels at the sand-mud interface. **B.** The same burrow system shown from a different angle demonstrating that much of the sediment volume was unbioturbated.

3.5.2. Geochemical changes associated with burrowing

Samples were taken from mud-lined walls (from Tank 2; Plate 3.1B) and the organic fraction analysed for its total organic carbon content and stable carbon isotopes. These macro-biologically redistributed mud-rich samples were compared with unbioturbated fine-grained sediment collected from the same levels within the mesocosm (Fig. 3.5).

3.5.2.1. TOC (Fig. 3.5A)

Unbioturbated mud shows the lowest concentrations of organic carbon (mean 7.4±1.9% TOC, range 5.22–9.7% TOC). Burrow lining pellets have higher values (mean 9.8±4.7% TOC, range 1.10–14.78% TOC). These results indicate that organic carbon considerably richer in the burrow wall compared to the host sediment. The highest TOC value in this data set was found in a burrow pellet (sample UG1; 14.8% TOC). The lowest TOC value was found from an unbioturbated sample taken from a burrow floor where a shrimp constructed a burrow on top of a mud layer (sample BH1; 1.10% TOC).

3.5.2.2. $\delta^{13}C_{org}$ (Fig. 3.5B)

The unbioturbated samples show uniform $\delta^{13}C_{org}$ values (mean -23.5±0.05‰, range -23.44‰ to -23.54‰). Data acquired from the biologically manipulated mud samples (burrow walls) had a greater spread of values (mean -23.5±0.3‰, range -23.20‰ to -23.96‰). Most of the bioturbated samples are similar to the unbioturbated values or heavier (Fig. 3.5B). The average value of the bioturbated samples in made lighter by a highly negative value for UG1 (Fig. 3.5B). This is considered an anomalous reading

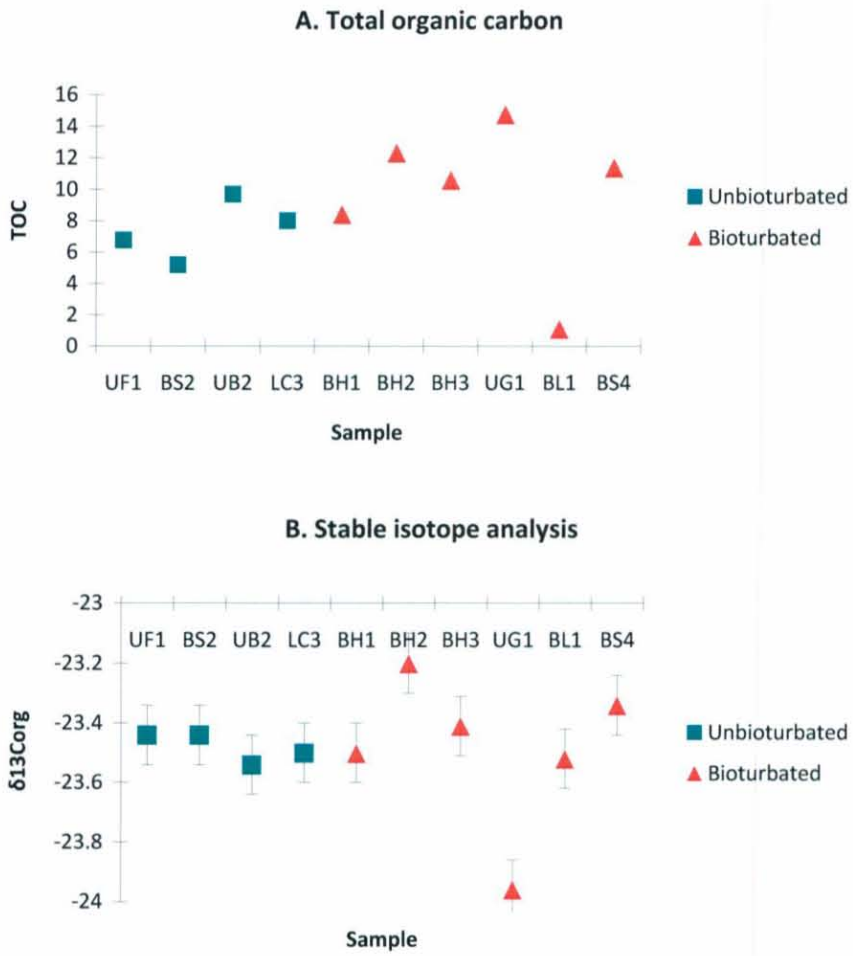


Fig. 3.5. Graphs showing the geochemical data acquired from the burrow seen in Tank 2. **A.** TOC data. **B.** $\delta^{13}C_{org}$ data (see text for discussion of results).

(discussed below). Both the highest and lowest values of $\delta^{13}C_{org}$ were found in the burrow walls. A mud pellet (sample UG1) had the most negative value with -23.96‰.

3.6. Discussion

This paper attempts to provide an explanation for the abundance of burrows along sandstone-mudstone interfaces commonly observed in turbidite systems (e.g. Fig. 3.1; Phillips *et al.* 2011). This distribution can potentially be explained by: (1) a need for burrow-stabilizing mud-lined walls in unstable (looseground) substrates (Weimer & Hoyt, 1964; Shinn, 1968; Frey *et al.* 1978; Miller & Curran, 2001); (2) concealed firmgrounds that are impenetrable to the burrowing organism focusing burrow activity at the surface of a lithological heterogeneity (Miller & Curran, 2001); (3) toxicity of a buried horizon (e.g. high concentrations of hydrogen sulfide) that act as a biogeochemical barrier to bioturbation (Volkenborn *et al.* 2007); and (4) the search for organic carbon in sediments buried at depth.

Observations from the Grès d'Annot Formation and our mesocosms provide evidence that allows us to test these various possibilities. A mud-free shaft of *Ophiomorpha* over 2 m deep through a massive turbidite (Fig. 3.1D) suggest that stabilization of the burrow wall with mud pellets was unnecessary to ensure burrow stability in the loose turbidite sand (*contra* Shinn, 1968). Hydrodynamic energy was minimal in the mesocosms but the sands were loose, being free of organic material, mucous, and microbial extracellular polymeric substances. It is possible that *N.*

californiensis could have constructed its pellet-lined burrows for burrow reinforcement. In regions without mud linings, however, shrimp were able to stabilize the burrow without collapse (Plate 3.1C); indicating that pellets are not necessary for burrow wall stabilization.

Bioglyphs found on *Thalassinoides* demonstrate the presence of a concealed firmground (Fig. 3.1C), probably produced by burial dewatering and early diagenesis of the underlying clay-rich sediment. The preservation of burrows in full relief suggests that excavation of a concealed firmground was not a significant impediment to burrowing (Fig. 3.1C).

Visual and CT imaging data indicate a systematic burrow distribution, with *Neotrypaea californiensis* preferentially burrowing along sand-mud interfaces (Plate 3.1F-G; Fig. 3.4). Our captive specimens display similar burrowing behaviour to ancient wild *Ophiomorpha* and *Thalassinoides* tracemakers. The distribution pattern of burrows is consistent with observations made on the distribution of *Ophiomorpha* and *Thalassinoides* seen in ancient turbidite settings (Fig. 3.1; Chapter 2; Uchman, 1995, 1998, 2009; Phillips *et al.* 2011). It has previously been suggested that the tracemakers of *Ophiomorpha* and *Thalassinoides* in ancient settings were feeding off microbes in fine-grained organic carbon-rich sediment (carbon in biofilms), rather than the organic carbon itself (MacGinitie, 1978; Miller, 1984; Bromley, 1996; Uchman, 2009; this paper). The data presented in this study presents several lines of evidence for microbial communities being an important factor influencing, and influenced by, the distribution of ancient tracemakers.

1. The reconstruction in Fig. 3.4 shows that most of the sediment volume is devoid of burrows. This could indicate that once burrows were constructed, no further expansion of the burrow networks took place. The low bioturbated volume suggests that deposit feeding from organic carbon in fine-grained sediment was not a primary source of nutrition for *Neotrypaea californiensis* as much of the mud layers remained unutilized. Serial slicing of sediment from the tanks demonstrated no evidence of filled in or collapsed burrows; a sign that the unbioturbated tank volume might have been previously mined (Fig. 3.6). It is postulated that deposit feeding was not the primary source nutrition for the shrimps and they utilized another food source that did not require expansion of the burrow network. Microbial farming is a possible source of nutrition which would not require continual burrowing activity represented by the behaviour of *N. californiensis* in our study.
2. *Neotrypaea californiensis* were seen to ingest fine-grained sediment from the burrow-lining pellets (Plate 3.1F). This behaviour was regularly seen in the mesocosms and suggests that the pellets acted as a food source for the shrimp. The sediment is inferred to have been enriched in microbial biomass and DOC (based on relatively high TOC values; Fig. 3.5A). Observations made of the shrimps recall that the animals exploited a different pellet each feed, perhaps allowing the microbial communities to recover between feeding sessions. This is the first time such behaviour has been observed in laboratory experiments and may provide an explanation for the pelleted wall of *Ophiomorpha*, particularly in deep-sea turbidite settings.

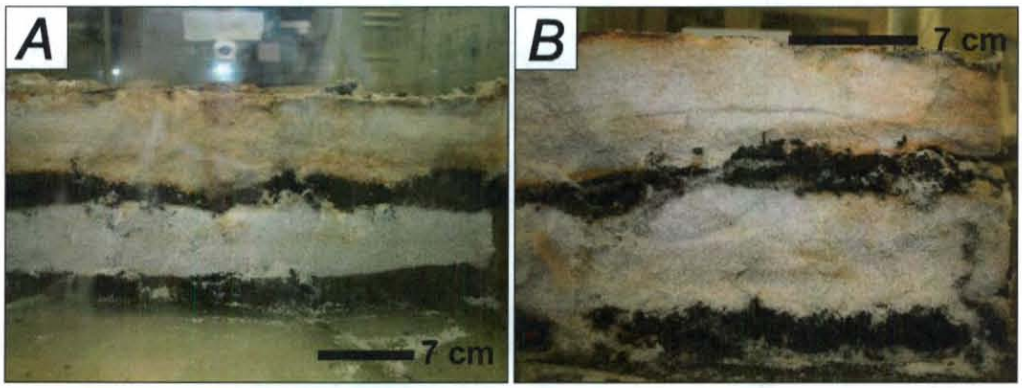


Fig. 3.6. Photographs taken during the excavation of tank 2. **A.-B.** During the excavation the mud interbeds were found to be structureless. No signs of burrow collapse or backfill were found in the fine-grained interbedded muds. These observations support the interpretation from the CT reconstructions in Fig. 3.4 that suggests that the majority of the sediment volume was not burrowed by *Neotrypaea californiensis* and that the animals did not extend their burrow network after it was constructed (see Fig. 3.4). Both this figure and Fig 3.4 suggest that deposit feeding was not the main mode of feeding for *N. californiensis* during its lifetime in the tanks.

3. The geochemical data presented herein could also support the hypothesis that microbial farming was the key mode of nutrition during the lifetime of the burrowing organism. *N. californiensis* was seen to sift material using its maxillipeds, either sifting the grains to feed on organic carbon directly or possibly selecting organic carbon-rich grains to make into pellets, suitable for sites of significant microbial colonization. Increased TOC values from burrow walls could have been derived from an increased microbial biomass and microbially generated DOC. Microbially rich burrow walls have been recorded from other studies (Hines & Jones, 1985; Dufour *et al.* 2008). Higher TOC values are not considered to be a result of incorporation of faecal material into the burrow lining or pellets. *N. californiensis* faecal pellets are stiff, rod-shaped packages, 1 mm in diameter and up to 5 mm long (Powell, 1974). These were not found in burrow pellets or linings nor were animals observed placing faecal material into their burrow walls. The highest TOC values were found from burrow-lining pellets (Fig. 3.6A). This organic carbon could either be: (1) mechanically sorted from the host sediment and concentrated into the wall-lining pellets, or (2) a result of increased microbial biomass. $\delta^{13}C_{org}$ data show a mostly heavier set of values in the burrow wall than from the non-bioturbated material (Fig. 3.5B). Positive deviations from the uniform values of the non-bioturbated samples are interpreted as evidence of isotopic fractionation occurring in the burrow walls. Heavier values are most likely due to aerobic microbial respiration, removing the lighter carbon isotope during metabolic processes (e.g. Hayes *et al.* 1989; Hayes, 1993, 2001; Olive *et al.* 2003). Only one value is significantly lighter relative to

unbioturbated mud samples and considered to be anomalous (sample UG1; Fig. 3.5B). The negative shift may indicate incorporation of C_3 terrestrial plant material into the burrow wall and used as a food source, or as a medium for microbial culturing. C_3 plants have an average $\delta^{13}C_{org}$ value of -27‰ (Cerling *et al.* 1989). Cold temperatures and plentiful ground water encourage the dominance of C_3 plants such as conifers (Wullshleger, 1993), debris from which is abundant in the organic-rich estuarine mud used in these mesocosms. Alternatively this more negative value could be due to anaerobic fractionation (sulphate reducing or methanogenesis, in a microenvironment within the pellets) producing enrichment in the lighter ^{12}C isotope (Hayes, 1993).

3.6.1. Finding deep-buried nutrition in turbidite systems

The location mechanism by which our shrimps and the ancient *Ophiomorpha* and *Thalassinoides* tracemakers found buried organic carbon-rich horizons is unclear. Sensory detection of organic compounds (including carbohydrates) has been observed in crustaceans (Prosser, 1961). The extent to which this detection method was used cannot be quantified in the ancient or in the present study. In the clean, organic-free sands of our mesocosms *Neotrypaea californiensis* did not have more than 7 cm of sand to burrow through to reach a source of nutrition. Turbidite sandstones are often much thicker. *Ophiomorpha* penetrating beds greater than 1 m thick have been described (Fig. 3.1D; Seilacher, 1962; Hubbard & Shultz, 2008; Phillips *et al.* 2011). One possible mechanism is a continued downward burrowing using a 'hit or miss' approach. When *N.*

californiensis encounters a barrier on its downward path it has been observed to burrow horizontally along the obstacle and then continue vertically downwards from the obstacle's edge (Miller & Curran, 2001). This behaviour can be interpreted as a strong instinct for vertical burrowing in search of nutrition. The *Ophiomorpha/Thalassinoides* tracemaker may also encounter an amalgamation surface between two sandstone turbidites (Fig. 3.2). The continued downward burrowing instinct of the tracemakers could be grain-size dependent and that during burrowing, the tracemaker sought interfaces with a sudden decrease in grain-size (i.e. from sand to mud) corresponding to the location of a possible organic-rich horizon. At amalgamation surfaces a grain-size change would not be accompanied by an increase in organic carbon content. As a result the *Ophiomorpha* tracemakers appear to cease burrowing (Fig. 3.2). This may suggest that the search strategy for identifying organic carbon-rich horizons in turbidite successions is granulometric, coupled with a drive for vertical downward burrowing until a fine-grained horizon is found or the search is abandoned.

3.6.2. Pre-adaptations to deep marine colonization by thalassinids

Thalassinid crustaceans are an adaptable group of organisms found in a many depositional settings, bathymetries, and depths within the sediment (Dworschak, 2000). Intertidal thalassinid species such as *Neotrypaea californiensis* are adapted to oxygen-poor or anoxic pore water conditions (Thompson & Pritchard, 1969; Grimm & Föllmi, 1994). Subaerial exposure during low tides leaves burrows isolated from oxygenated seawater which quickly become hypoxic (Thompson & Pritchard, 1969; Swinbanks &

Luternauer, 1987). Thalassinids have demonstrable physiological adaptations including redox tolerance and resilience to the effects of lowered oxygen. *N. californiensis* has a low metabolic rate and can survive anoxia for 138±27 hours (5.7 days; Thompson & Pritchard, 1969). Thalassinids show the ability to sense oxygen concentration. Under low oxygen levels *N. californiensis* was observed to rhythmically beat its pleopods in an attempt to ventilate its surroundings and increase its oxygen supply (Farley & Case, 1968).

It has been suggested that thalassinids could survive transportation in turbidity currents, enabling them to construct burrow networks in offshore event beds (Föllmi & Grimm 1990; Grimm & Föllmi 1994). Thalassinids could exploit possible organic carbon-rich horizons buried beneath the deposits of the turbidity current that transported them. The 'doomed pioneer' hypothesis was proposed in which shrimp lived only for a short period before conditions became lethal (Föllmi & Grimm 1990; Grimm & Föllmi 1994). This does not, however, take into account the possibility that burrowing decapods were already inhabitants of the deep seafloor (cf. Hartnoll *et al.* 1992; Kern & Warme, 1974; Hayward, 1976; Uchman, 2009). The adaptations of thalassinid crustaceans to low oxygen conditions and short periods of anoxia certainly suggest that thalassinids would be able to survive such events but also indicate that they can be a natural component of the deep-sea fauna. It is entirely possible that the ancient progenitors of *Ophiomorpha* and *Thalassinoides* in deep-water palaeoenvironments could have been decapod crustaceans found as part of the natural deep-water benthos.

3.7. Conclusion

The geological record preserves *Ophiomorpha* and *Thalassinoides* in high abundances at sandstone-mudstone interfaces in turbidite systems (Chapter 2; Uchman, 1995, 2009; Phillips *et al.* 2011). This paper and the experiments presented herein provide a model for the apparent preference for burrowing along lithological contacts and propose an explanation for tracemaker ethology in these instances. Inter-turbidite and hemipelagic muds at the base of the basin slope are commonly buried beneath metres of rapidly deposited turbidite sand. From an ecological perspective, turbidite events produce an organic matter-poor sediment-water interface: clean sand buries organic carbon-rich muds to a depth inaccessible to many benthic organisms. Exploitation of these deeply buried food stores is thus restricted to deep-burrowing macrofauna such as the *Ophiomorpha* and *Thalassinoides* tracemakers.

Though the biological affinities of the *Ophiomorpha* and *Thalassinoides* tracemakers cannot be confidently inferred from the trace fossil record, similarities in burrow structure and morphology between ancient and modern examples lead us to conclude that the tracemakers were physiologically and behaviourally comparable with modern thalassinid shrimp (Fig. 3.1A-E; Frey *et al.*, 1978; Uchman, 2009). Previous studies on *Ophiomorpha* and *Thalassinoides* considered their tracemakers to have been either suspension feeders (e.g. Anderson & Droser, 1998) or deposit feeders (e.g. Weimer & Hoyt, 1964; Uchman, 1995). Deposit feeding forms are interpreted to have fed directly on organic carbon in fine-grained sediment (Wetzel, 1991) or indirectly on microbial

biomass and DOC produced by microbial respiration (MacGinitie, 1978; Miller, 1984; Uchman, 2009). We have presented evidence herein for an alternative mode of feeding: microbial cultivation. It is proposed that burrow-lining pellets of ancient *Ophiomorpha* in deep-sea turbidite settings could have been used as a medium for cultivating microbes.

Observational data and CT imagery of our mesocosm experiments suggests that *Neotrypaea californiensis* preferentially burrow along sand-mud interfaces (Plate 3.1; Fig. 3.4). Geochemical data shows increased total organic carbon values from the burrow walls of the *N. californiensis* compared to unbioturbated samples as well as evidence for aerobic microbial respiration within burrow walls. Relatively high TOC values in burrow walls are probably due to the organism actively selecting and packaging organic carbon-rich sedimentary particles into its burrow wall pellets. This provides a suitable medium for microbial cultivation either to feed on the microbes themselves or DOC produced by them as they respire. Heavier $\delta^{13}C_{org}$ values in wall pellets infer isotopic fractionation by microbial processes (Fig. 3.5B). Bioirrigation of deep burrows maintains geochemical gradients allowing aerobic microbes to respire and break down refractory POC to bio-available DOC for consumption by the burrow occupant. Our data could provide an explanation for the preferred distribution of *Ophiomorpha* and *Thalassinoides* along sandstone-mudstone interfaces in ancient turbidite systems. Microbial farming in the burrow-lining pellets of *Ophiomorpha* is postulated to be able to maintain a community of deep-burrowing organisms in deep-sea, deep-sediment settings.

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CHAPTER 4

Ichnfabrics and biologically mediated changes in clay mineral assemblages from a deep-water, fine-grained, calcareous sedimentary succession: an example from the Upper Cretaceous Wyandot Formation, offshore Nova Scotia

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CHAPTER 4

Ichnofabrics and biologically mediated changes in clay mineral assemblages from a deep-water, fine-grained, calcareous sedimentary succession: an example from the Upper Cretaceous Wyandot Formation, offshore Nova Scotia

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Abstract

The Upper Cretaceous Wyandot Formation is a 400 m thick reservoir facies composed of autochthonous fine-grained calcareous mudstone deposited in an outer shelf to upper bathyal setting. The formation contains two lithofacies: (1) homogeneous chalk; and (2) an interbedded kaolinite-bearing, calcareous claystone. Ichnofabric analysis reveals trends of environmental deterioration and amelioration linked to fluctuations in the supply of organic matter to the sediment-water interface. Increased supply of organic matter led to a rising of the redox front and low porewater/sediment oxygenation excluding many endobenthic organisms. Mineralogical and textural differences between burrow fill and host sediment demonstrate that bioturbation affects sediment texture by altering authigenic clay mineral assemblages. Clay mineral assemblages in burrow fills are more

diverse than in the host sediment, most likely a result of low temperature authigenesis in the digestive system of deposit feeding endobenthos. These findings show that deposit feeding endofauna can alter the abundance and diversity of clay mineral assemblages in fine-grained calcareous sediments.

4.1. Introduction

Deep-sea settings away from terrigenous input are aerially the most extensive depositional environment for fine-grained material (Ekdale *et al.* 1984). In settings above the calcite compensation depth (CCD) almost all the material reaching the ocean floor is sourced from the photic zone (Brasher & Vagle, 1996). Foraminifers and nannoplankton may be incorporated in faecal pellets and amalgamate into macroaggregates or 'marine snow' for transport to the seafloor (Schlanger & Douglas, 1974; Gooday & Turley, 1990; Brasher & Vagle, 1996). Steady-state pelagic conditions are typified by lower sediment accumulation rates and productivity-derived sediments compared to settings with more terrestrial influence (Doeven, 1983; Bromley & Ekdale, 1984; Wetzel, 2002). Consequently, fine-grained pelagic sediment may be bioturbated, possibly multiple times, by benthic organisms before being buried beneath the zone of bioturbation (Ekdale & Bromley, 1991; Locklair & Savrda, 1998).

Animals live and feed at different depths in the substrate based on species-specific needs such as sediment firmness, oxygenation, and organic matter content (Ausich & Bottjer, 1982; Savrda & Bottjer, 1986; Wetzel, 1991). This vertical partitioning of the

sediment is seen in box cores taken from numerous localities in modern oceans and in the geological record from deep marine settings (Wetzel, 1983, 1991; Ekdale & Bromley, 1984, 1991; Ekdale *et al.* 1984; Locklair & Savrda, 1998). Bioturbated pelagic sediment can be defined in three layers: an upper mixed layer, an intermediate transition layer, and a lower historical layer (Fig. 4.1; Berger & Heath, 1968; Berger *et al.* 1979; Wetzel, 1983; Savrda & Bottjer, 1989). The mixed layer is a thin zone of soupy sediment, typically 3-15 cm thick (Savrda & Bottjer, 1989), which is continually bioturbated by deposit feeding benthic animals (Berger *et al.* 1979; Ekdale & Bromley, 1991). As a result, the primary sedimentary fabric of the sediment is removed (from the geological record) by the burrowing activity of the endobenthic community (Ekdale & Bromley, 1991; Locklair & Savrda, 1998). The transition layer contains feeding and dwelling structures of organisms that burrow deeper in the sediment (Savrda & Bottjer, 1989). Many generations of burrowing organisms may be preserved in the transition layer leading to complex overprinting that can be difficult to subdivide into component ichnocoenoses (Ekdale & Bromley, 1983a, 1984; Bromley & Ekdale, 1991; Wetzel, 1991; McIlroy, 2004). The historical layer lies below the depth of bioturbation (Goldring, 1995). The historical layer enters the rock record as a modification of the mixed layer: a mottled fabric formed by biodeformational structures with deep-tier and elite trace fossils from the transition layer superimposed (Fig. 4.1; Savrda & Ozalas, 1993).

This paper considers deep-water, fine-grained carbonates, principally composed of productivity-derived calcareous material. The effects of bioturbation on such deposits are illustrated in the chalks and interlayered marlstones of the Upper Cretaceous Wyandot Formation, offshore Nova Scotia. This paper is the first to document, in detail, the trace

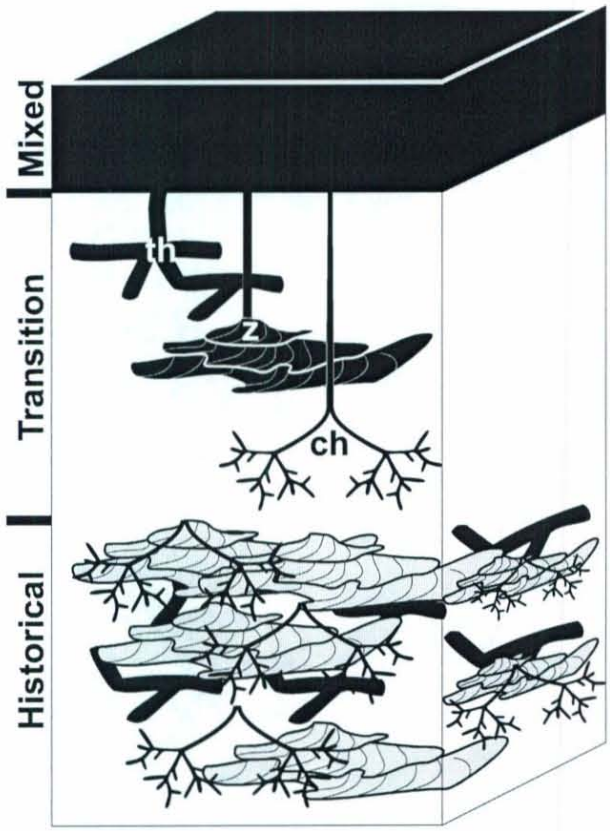


Fig. 4.1. Schematic diagram showing the generalized stratigraphy and archetypical tiering of trace fossils as can be found under steady-state conditions. This model is based on the tiering of trace fossils found in the Wyandot Formation. *Thalassinoides* (th) is overprinted by deeper-tier *Zoophycos* (z) which is overprinted by the deepest-burrowing *Chondrites* constructor (ch).

fossils and ichnofabrics of the Wyandot Formation and examines changes in ichnofabric related to palaeoenvironmental perturbations. The Wyandot Formation is a reservoir facies with an oil and gas show (Wielens *et al.* 2002; Ings *et al.* 2005). This paper show cases the utility of ichnofabric analysis to identify environmental changes in reservoir facies and how endobenthic animals affect geotechnical properties of the sediment. Environmental changes interpreted through changes in the palaeobenthic community and ichnofabrics can be used to illustrate changes in depositional conditions that can have an effect on reservoir facies. There is an increasing contribution of work on the impact of bioturbation on reservoir facies (Gingras *et al.* 1999, 2007; Pemberton & Gingras, 2005; Tonkin *et al.* 2010) but there are very few studies focussed on chalk reservoirs compared to siliciclastic systems. The effect bioturbation has on the texture and mineralogy of fine-grained calcareous sediments is also assessed. This is of particular interest since biologically induced textural heterogeneities have significant controls on reservoir quality (McIlroy *et al.* 2003; Pemberton & Gingras, 2005; Tonkin *et al.* 2010).

4.2. Regional geology

The Scotian Shelf is located on the continental margin of south-eastern Canada covering an area of 300,000 km^2 and extending for 500 km along the Scotian Margin (Fig. 4.2; Hansen *et al.* 2004). The Wyandot Formation is a 400 m thick Upper Cretaceous (Santonian-Maastrichtian) succession of autochthonous chalk and interlayered marlstone (Wielens *et al.* 2002). Using the tripartite classification of chalk (based on the

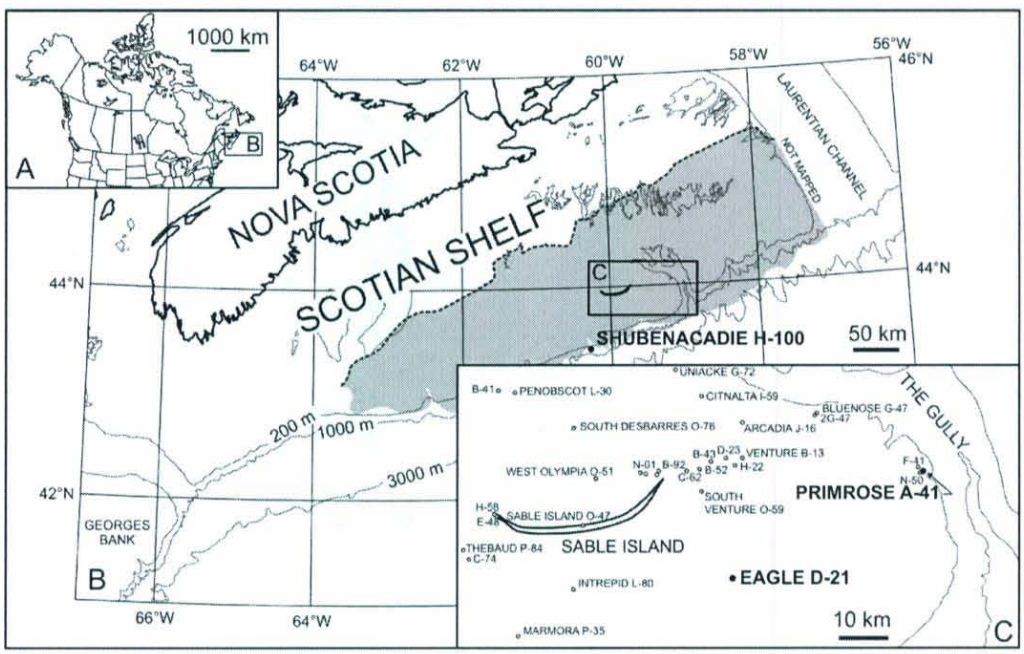


Fig. 4.2. A.-B. A location map of the Scotian Shelf along the continental margin of eastern Canada. **C.** Location of petroleum exploration wells, notably the Eagle D-21, Primrose A-41, and Subenacadie H-100 wells. The shaded region indicates the extent of the Wyandot Formation on the Scotian Shelf. The dashed landward boundary of this region indicates where the Wyandot Formation subcrops beneath Quaternary strata. Modified from Ings *et al.* (2005).

depositional mechanism) the Wyandot Formation is a Category I chalk (i.e. autochthonous in origin; Brasher & Vagle, 1996).

In the modern ocean calcareous ooze (incipient chalk) is deposited above the CCD in water depths of 2-4.5 km, and distal to terrigenous sources (Ekdale & Bromley, 1983b). The Wyandot Formation was deposited below storm wave base in an offshore shelf to upper slope setting (Wade *et al.* 1995; Wielens *et al.* 2002). A water depth of 150-200 m is implied from the abundance of the coccolith species *Lucianorhabdus cayeuxii* (Doeven, 1983). Newly deposited calcareous ooze has a primary porosity of 70-80% (Schlanger & Douglas, 1974) which can be preserved by diagenesis, over-pressuring, and hydrocarbon saturation (Brasher & Vagle, 1996). The Wyandot Formation records porosities of 15-35%, having been buried to depths less than 1.5 km (Ings *et al.* 2005) favourable for hydrocarbon reservoir facies. The Scotian Shelf has been targeted for hydrocarbon exploration and both oil and gas have been discovered in the Wyandot Formation and the Petrel Member of the underlying Dawson Canyon Formation (Fig. 4.3; Wielens *et al.* 2002). Despite these finds the Wyandot Formation is understudied compared to the underlying Jurassic and Lower Cretaceous reservoirs (Ings *et al.* 2005).

The origins of the Scotian Shelf can be traced to the break-up of Pangea and the Late Triassic to Middle Jurassic deposition of syn-rift sediments (Wade & MacLean, 1990; Wade *et al.* 1995). These include salt beds precipitated from shallow hypersaline seas before marine transgressions resulted in the deposition of dolomite and limestone (Argo and Iroquois Formations on Fig. 4.3; Wade, 1981). These are overlain by interbedded marine sandstone and shale as the initiation of seafloor spreading linked to

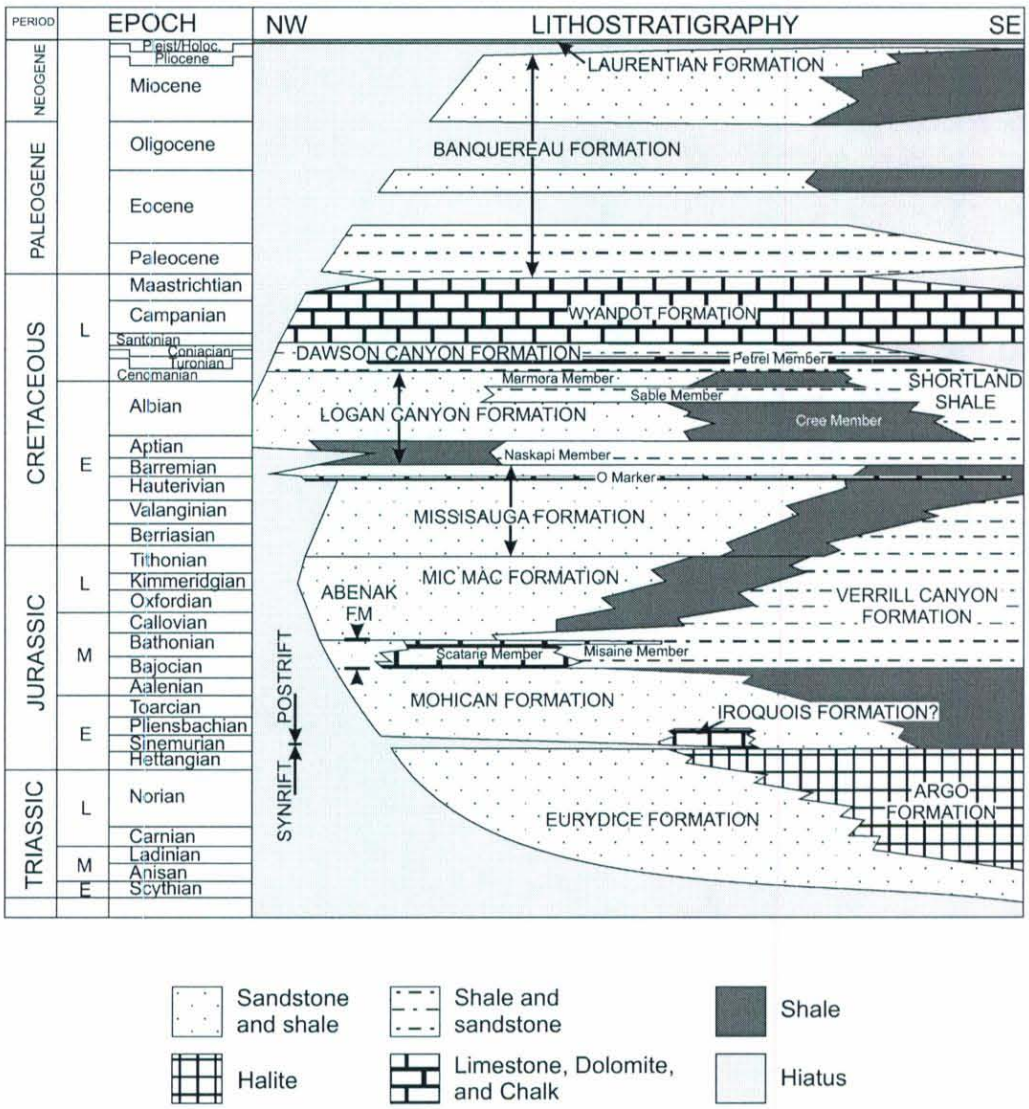


Fig. 4.3. Generalized Scotian Shelf lithostratigraphy. Redrawn from Ings *et al.* (2005).

the opening of the proto-North Atlantic increasing accommodation space (Abenak, Mic Mac, Verrill Canyon Formations on Fig. 4.3; McIver, 1972; Wade, 1981). Post-rift facies were deposited in open marine conditions after marine transgressions and further tectonism increased accommodation space. The Scotian Shelf shows gradual deepening through the later Mesozoic with the deposition of, amongst others, the Wyandot Formation (McIver, 1972; Eliuk, 1978; Wade, 1981). The Wyandot Formation is a post-rift formation deposited distal to terrigenous sources. Latest Cretaceous and Early Cenozoic siliciclastic mudstone cap the Wyandot Formation and continue through the Cenozoic (the Banquereau and Laurentian Formations on Fig. 4.3; Wade, 1981).

4.3. Methods and dataset

This paper examines split cores from three wells drilled through the Wyandot Formation housed at Canada-Nova Scotia Offshore Petroleum Board, Dartmouth, Nova Scotia. These wells are Eagle D-21, Primrose A-41, and Shubenacadie H-100. Each well was drilled to different depths in the Wyandot Formation; the Eagle D-21 well being the deepest, then Primrose A-41, followed by shallowest drilled well, Shubenacadie H-100. There is no stratigraphic overlap between the wells. Cores were described sedimentologically and ichnologically on a bed-by-bed scale to produce an integrated ichnological-sedimentological analysis (see methodology in McIlroy, 2008). This paper discusses changes in depositional conditions interpreted through observed changes in ichnofabric, an ichnofabric being "all aspects of the texture and internal structure of the

bed resulting from all phases of bioturbation" (Ekdale & Bromley, 1983, p. 110; see also McIlroy, 2004).

Table 4.1 lists the ichnogenera found in the Wyandot Formation. Identification of trace fossils in cores can be problematic since they can only be viewed in two dimensions. Concomitantly, some diagnostic information, such as wall structure, goes unseen which can make identification subjective (McIlroy *et al.* 2009). To eliminate as much misinterpretation as possible trace fossils were described at the ichnogenus level only (following Wetzel, 1987).

The bioturbation index (BI) is a semi-quantitative method of describing the amount of bioturbation on a graded scale; BI 0 having preservation of all primary fabric to BI 6 being complete burrow homogenization (Goldring, 1995). Low lithological contrast between trace fossils and host sediment due to textural and chemical purity of the chalk makes identification difficult. Selected photographic images were digitally enhanced to improve contrast between burrow fill and surrounding sediment.

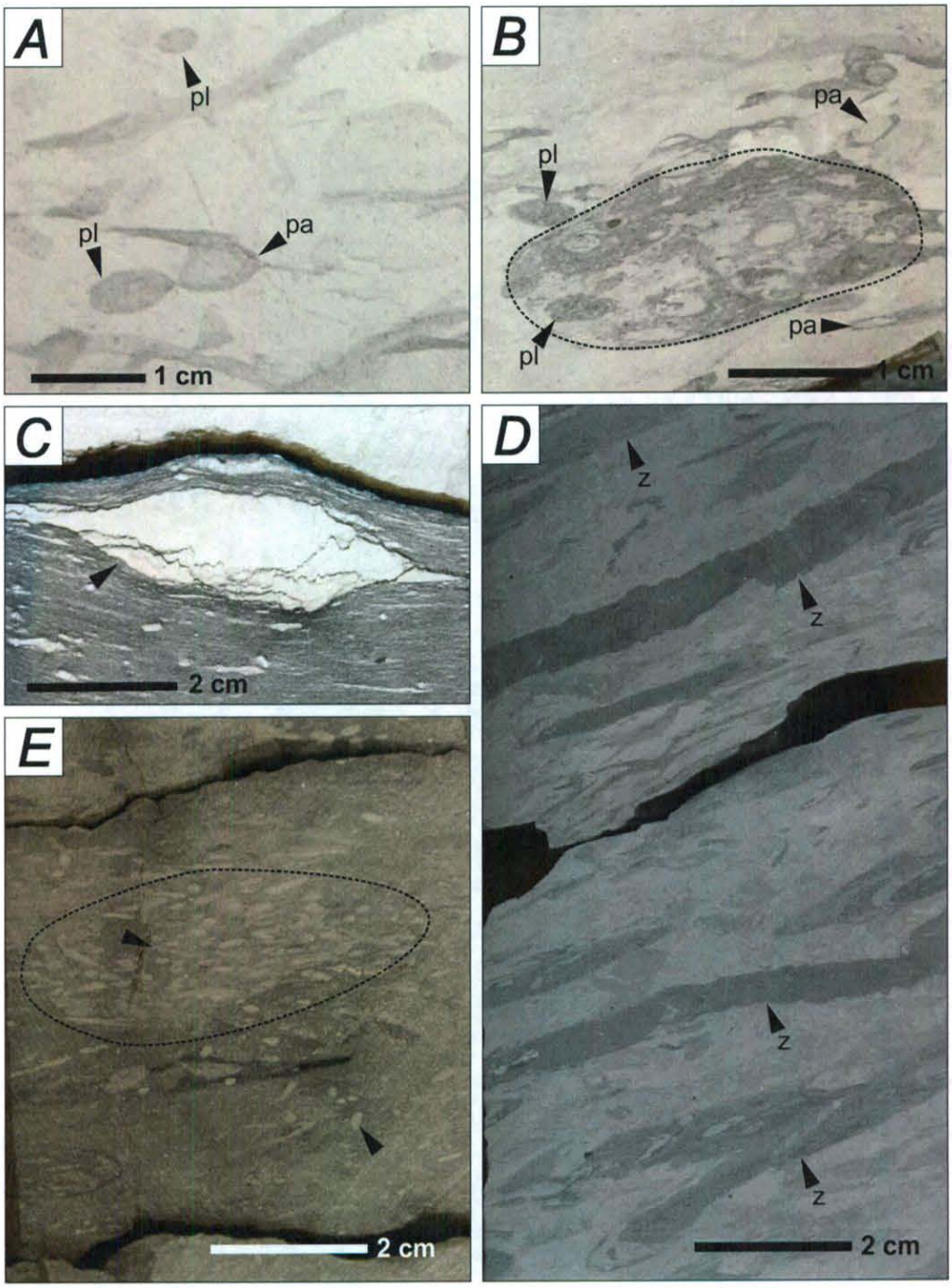
Percentage abundances of foraminifers and authigenic and detrital grains were obtained from thin sections by point counting. Areas of core that showed the greatest lithological and ichnological interest were sampled for petrographic and backscattered electron imagery. Thin sections were analyzed in a FEI Quanta 400 with a Bruker XFLash 4010 energy discriminating (EDX) X-ray detector at Memorial University of Newfoundland.

There are no marker beds in the Wyandot Formation (sedimentological or geophysical) that can be used for regional correlation as primary sedimentary fabric has been removed by burrowing organisms. Bioturbation also disrupted sedimentary bedding

Ichnogenera	Description	Remarks
Chondrites (Figs 4.5C, 4.7A-D, 4.8C & Plate 4.1E)	Circular, ovoid, or filamentous tubes. Horizontal and vertical components, straight and curved. Burrows 1-3 mm in diameter. Filled by structureless chalk or marlstone. *Chondrites* overprint all ichnogenera. Abundant.	These specimens conform in size and character to the *"regularly ramifying tunnel structures"* described by Kennedy (1967; p. 148) of the English Cretaceous chalk and northern European chalks (Ekdale & Bromley, 1983a).
Palaeophycus (Plate 4.1A-B)	Sub-circular tubes, c. 10 mm. Burrow wall 1-2 mm thick and made of muddier calcareous material compared with burrow fill and host sediment. Structureless burrow fill. Common.	*Palaeophycos* is described as a lined tube made in oxygenated sediments by veriform organisms maintaing an open connection to the surface (Pemberton & Frey, 1982).
Planolites (Figs 4.5A-B, 4.7A & Plate 4.1A-B)	Sub-circular and lenticular horizontal tubes 5-12 mm wide. Unlined. Homogeneous fill composed of calcareous material richer in clays compared to the host sediment. Common.	These burrows resemble *Planolites* from modern sediments: unlined, horizontal tunnels (Wetzel, 1983; Ekdale *et al*. 1984).
Teichichnus	Series of concave-upward stacked laminae (spreite) 10 mm wide. Spreiten darker (more clay-rich) than inter-spreite areas and host sediment. Last causative burrow (sub-circular, structureless fill) preserved on top of spreiten. Common.	Similar in morphology to the *Teichichnus* described by Wetzel (1987, p. 827), roof gutters stacked on top of each other with the last open burrow on top.
Thalassinoides (Figs 4.5A, 4.7A & Plate 4.1B,C,E)	Oval and lenticular horizontal burrows 12-40 mm wide. Unlined. Burrow fills of structureless chalk or marlstone. Abundant.	*Thalassinoides* resemble the forms described by Ekdale & Bromely (1983a, 1984): sub-circular burrows, unlined, >1 cm wide
Zoophycos (Figs 4.5A, 4.7A,D,E & Plate 4.1D)	Burrows 2-10 mm thick, commonly width of vertical core (7-10 cm). Horizontal to oblique lobes (inclined at up to 45°). Burrow fill structureless or have laterally directed spreiten (Fig. 4.4E). Structureless fill is probably an effect of the geometrical relation between spreiten fill and core surface. *Zoophycos* fill usually darker (muddier) than host sediment. Abundant.	Wyandot *Zoophycos* are comparable to the forms seen in the Upper Cretaceous Kjølby Gaard Marl of Denmark (Ekdale & Bromley, 1983, 1984, 1991) and from modern box cores taken from numerous deep-water environments (Wetzel & Werner, 1981; Wetzel, 1983, 1984; Ekdale *et al*. 1984).

Table 4.1. Trace fossil ichnogenera described from the Wyandot Formation.

so there are no identifiable colonization surfaces unlike other coeval Cretaceous chalk deposits (Ekdale & Bromley, 1984; Frey & Bromley, 1985; Locklair & Savrda, 1998). Consequently, the depth of bioturbation could not be unequivocally established from objective sedimentological criteria. A colonization order can be established by cross-cutting relationships. The *Thalassinoides* constructor was one of the first animals to burrow into the sediment. In the Wyandot Formation *Thalassinoides* is a shallow-tier trace fossil overprinted by other shallow-tier and deep-tier trace fossils related to younger stratigraphic levels such as *Planolites* and *Palaeophycus* (Plate 4.1A-B). The *Thalassinoides* tracemaker was probably a decapod crustacean which maintained an open connection to the surface (Frey *et al.* 1978). *Planolites* tracemakers did not maintain a permanent open connection to the sediment-water interface so were restricted to the oxic mixed layer (Plate 4.1A-B; Pemberton & Frey, 1982). *Thalassinoides* is re-burrowed and overprinted by mixed layer ichnofauna such as *Planolites* and *Palaeophycus* (Plate 4.1B). *Zoophycos* is also seen to cross-cut *Thalassinoides,* but mutual cross cutting is not documented herein. This indicates that *Zoophycos* was emplaced after *Thalassinoides* and that the *Zoophycos* constructor was a deep-tier organism living and feeding at depth in the sediment (Weztel, 1983). The *Chondrites* animal was the last to burrow the sediment as evidenced by the fact that it overprints all other ichnogenera (Plate 4.1E). The *Chondrites* animal is frequently referenced as a deep burrower, burrowing below the redox zone possibly feeding with the aid of chemosymbiotic bacteria (Seilacher, 1990; Fu, 1991) maintaining an open connection to the water column (Ekdale, 1992). Low sedimentation rates (evinced from intense biological reworking of the sediment and overprinting of trace fossils) mean that the true number of burrow generations is not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resolvable. Descriptions below, however, demonstrate that with careful ichnofabric analysis trends can be seen in core that could potentially, with improved core-coverage, be used for correlation of semi-regional sedimentation events on the Scotian Shelf.

4.5. Lithofacies

Fine-grained sedimentary rocks can be divided into three key constituents: (1) autochthonous material (derived from *in situ* primary and secondary production or advected by currents); (2) allochthonous material (detrital components delivered to the accommodation space *ex situ*); and (3) authigenic products resulting from diagenetic reactions within the sediment during or after burial (Macquaker & Adams, 2003). Lithofacies are commonly characterized according to the abundance of these three constituents. Two lithofacies are recorded from the Wyandot Formation.

4.5.1. Lithofacies 1

This lithofacies is made of white to light-grey, very fine-grained, carbonate (chalk). There are no physical sedimentary structures due to bioturbation (BI 5-6). Ichnogenera include *Chondrites*, *Palaeophycus*, *Planolites*, *Teichichnus*, *Thalassinoides*, and *Zoophycos*. Macrofaunal diversity is low and restricted to fragments of inoceramid bivalves (*Inoceramus* sp.; Fig. 4.4A; Jansa & Wade, 1975). Prominent stylolites are seen in thick successions of white chalk (Fig. 4.4B). The stylolites are characterized by a thin

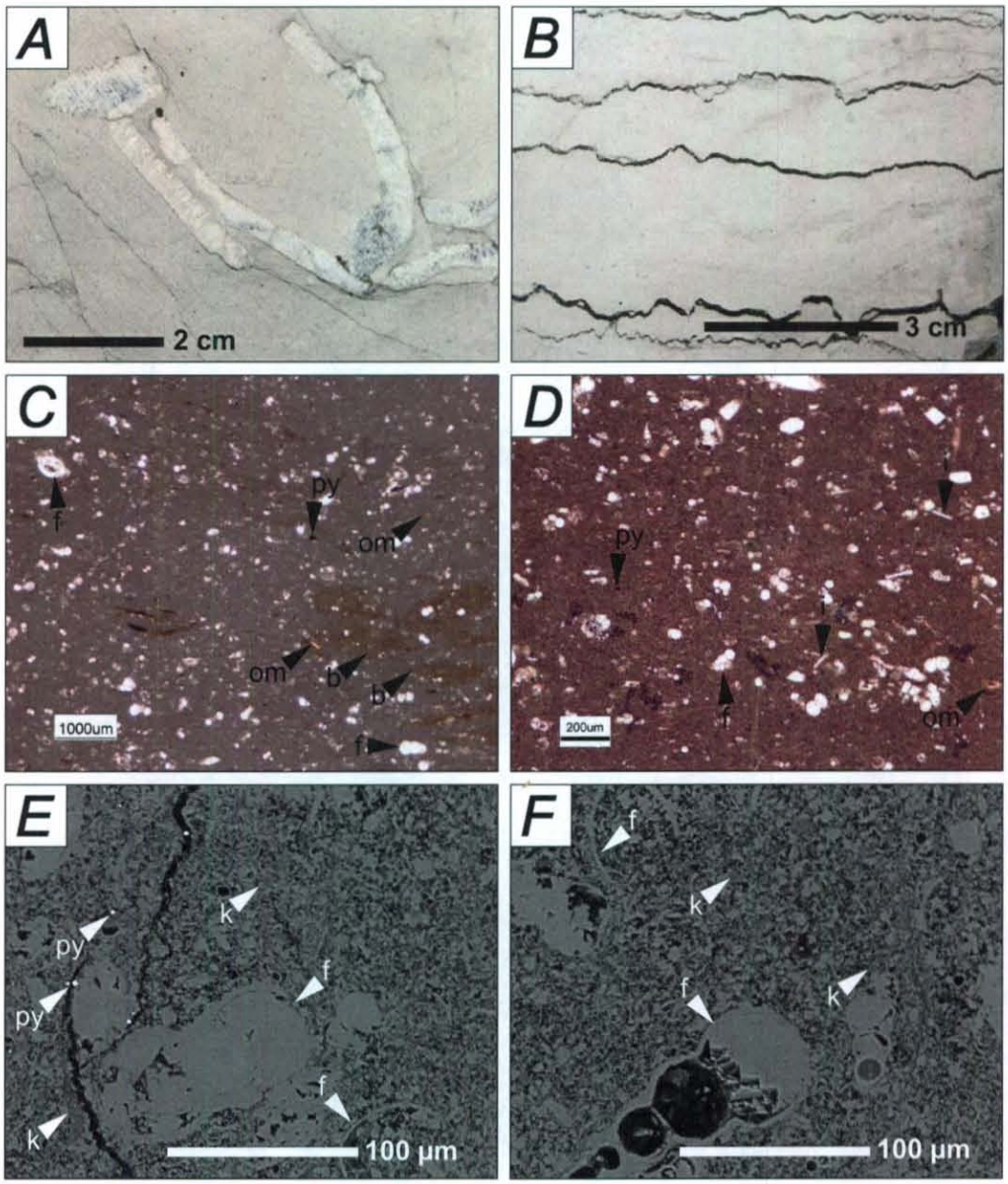


Fig. 4.4. Images of lithofacies 1. **A.** Fragments of the inoceramid clam, *Inoceramus*. Primrose A-41, core 5. **B.** Heavily stylolitized chalk (stylolites filled with organic-rich material). Eagle D-21, core 3. **C.** Abundant foraminifers (f). Pyrite (py) and organic matter (om) are scarce. Darker, clay-rich burrow fills are seen (b). Eagle D-21, core 1. **D.** Homogeneous calcareous matrix of lithofacies 1 with formainifers and rare inoceramid shell fragments (i). Eagle D-21, core 2. **E.** A backscattered image of the coccolith-dominated matrix with minor kaolinite (k) and pyrite crystals (py). Chambered foraminifers (f) are filled with calcite cement (in a *Planolites* burrow fill). Eagle D-21, core 1. **F.** SEM image showing calcite-cemented foraminifer chambers. Coccolith-dominated matrix with rare crystals of kaolinite (k). Eagle D-21, core 1.

insoluble residue of clay and organic material. They have a maximum thickness of 2 mm and maximum amplitude of 10 mm.

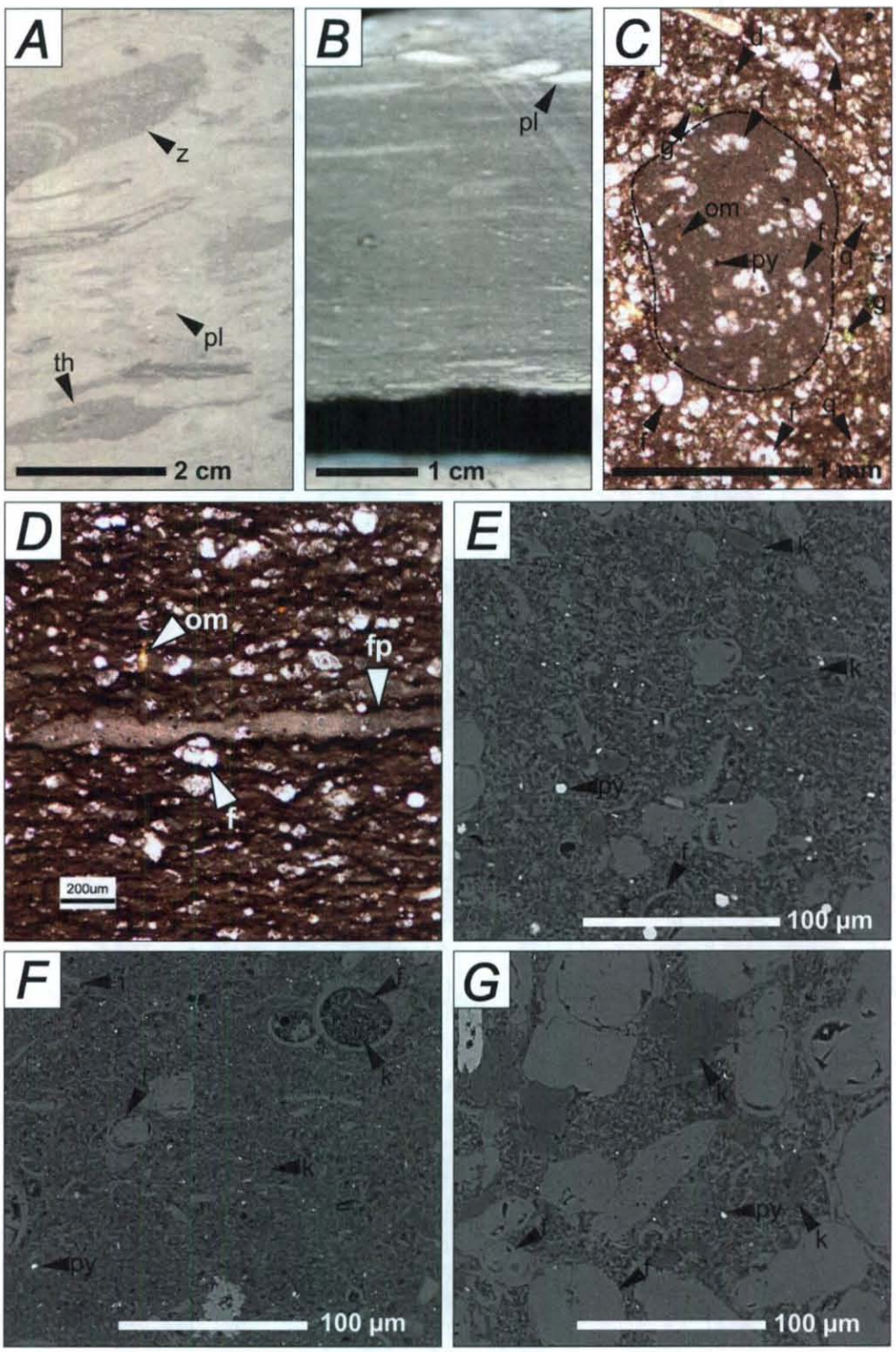
Under optical microscopy, the matrix is composed of a homogeneous, calcareous material (Fig. 4.4C-D). Calcareous, angular inoceramid shell fragments approximately 1 mm long are distributed randomly through the fine-grained matrix (Fig. 4.4D). No siliciclastic grains were seen under optical microscopy (Fig. 4.4C-D). Organic matter occurs in low abundance (<1%) as orange sub-circular grains or filaments 50-100 μm wide (Fig. 4.4D). Euhedral pyrite crystals are rare, less than 50 μm in diameter and also distributed randomly through the matrix (Fig. 4.4C). Foraminifer tests constitute 10-40 % volume of this lithofacies with the highest concentrations found within burrow fills (especially *Thalassinoides* and *Zoophycos*; Fig. 4.7). Foraminifers are found as both broken pieces and whole tests (Fig. 4.4C-F). SEM study of polished thin sections reveals a homogeneous matrix composed almost entirely of coccoliths (Fig. 4.4E). Kaolinite is rare and evenly distributed through the matrix; it is the only clay mineral found in lithofacies 1 (Fig. 4.4E-F). The mineralogy was determined by a combination of low back scattered electron coefficients, grain shape (bookish shapes), and low interference colours in XPL. EDS spectra showed Al and Si in a 1:1 ratio, characteristic of kaolinite (Deer *et al.* 1992). Less than 5% of the volume of lithofacies 1 is made of kaolinite (percentage obtained by point counting). Authigenic pyrite crystals are seen throughout this lithofacies at the SEM scale (Fig. 4.4C-E). Pyrite crystals are 1–5 μm wide and have angular shapes (Fig. 4.4E). There is no observable pattern to their distribution, neither preferentially clustering in burrow fills nor in the sediment. Following the nomenclature

of Macquaker & Adams (2003) this lithofacies is classified as a bioturbated, foraminifer- and coccolith-rich, calcareous claystone.

4.5.2. Lithofacies 2

Lithofacies 2 is a mid- to dark-grey, very fine-grained, calcareous mudstone (marlstone). Beds are typically 30 cm to 2 m thick and homogeneous (Plate 4.2A) but occur also as beds less than 5 cm thick which may have a wispy fabric made of thin (1 mm or less), closely spaced, incipient stylolites (Plate 4.2B). Stylolites are mid- to dark-grey and filled with a clay-rich material. They overprint burrows. In petrographic section, this wispy fabric shows numerous elongated faecal pellets and marine snow textures (Plate 4.2D; cf. Macquaker & Gawthorpe, 1993). Lithofacies 2 is completely bioturbated with no primary sedimentary fabric seen. A bioturbation index of BI 5–6 characterizes much of this lithofacies with sharp-walled burrows overprinting a burrow mottled sediment fabric (Plate 4.2A-C). Ichnogenera present include *Chondrites*, *Palaeophycus*, *Planolites*, *Thalassinoides*, and *Zoophycos* (Plate 4.2A-C).

Optical microscopy shows the matrix to be largely homogeneous carbonate with local concentrations of clay minerals, irregularly-shaped pyrite crystals up to 50 μm wide, and sub-circular organic detritus up to 100 μm wide (Plate 4.2C-D). Fragmented and intact tests of pelagic foraminifers comprise 30-60% of the rock volume (data obtained by point counting), with the highest concentrations of microfossils found in burrow fills, particularly *Thalassinoides* and *Zoophycos* (discussed in more detail below; Plate 4.2C; Fig. 4.7). Silt-sized quartz grains are an accessory component of the matrix (Plate 4.2C).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Rare arcuate fragments of calcitic bivalve shells approximately 20 μm long are seen; probably inoceramid fragments (being the only macrofauna identified in the Wyandot Formation; Plate 4.2C-D; Jansa & Wade, 1975). Backscatter SEM images show coccoliths are the primary constituent of the sediment matrix both in the host sediment and in faecal pellets (Plate 4.2E-G). Kaolinite (identified through low back scattered electron coefficients and diagnostic EDS spectra showing Al and Si in a 1:1 ration; Deer *et al.* 1992) is the most common clay mineral (Plate 4.2E-G). Point counting revealed that kaolinite constitutes up to 30% volume of lithofacies 2. The demonstrably diagenetic components of this lithofacies include euhedral rhombs of ferroan and non-ferroan dolomite, kaolinite (seen as booklets of kaolinite crystals), and pyrite crystals up to 10 μm wide (Plate 4.2E-G). Following the fine-grained sediment classification scheme of Macquaker & Adams (2003), this lithofacies is classified as a bioturbated, foraminifer- and coccolith-rich, kaolinite-bearing, calcareous claystone.

4.5.3. Palaeoenvironmental interpretations derived from lithofacies descriptions

The palaeoenvironmental interpretation of lithofacies 1 and lithofacies 2 is similar (Wielens *et al.* 2002). The absence of diagnostic shallow-water foraminifer and the high ratio of planktonic to benthic foraminifer in both lithofacies imply that they were deposited in deep-water (McIver, 1972), probably in an outer shelf setting (Doeven, 1983). This outer shelf setting shows that the Wyandot chalk was deposited in water depths much shallower than those that deposit chalk today (Ekdale & Bromley, 1983b). The dominance of coccoliths in the matrix of both lithofacies suggests the source for the

vast majority of the sedimentary particles was the photic zone with little clastic dilution. Kaolinite is the only clay mineral identified, and in low percentage volumes, with authigenic kaolinite contributing to the percentage volume. Lithofacies 1 is dominantly derived from autochthonous material delivered to the ocean floor by suspension setting from the photic zone. This could indicate that lithofacies 1 was either deposited under a water column with high primary productivity or at the end of a sediment transport path (due to minor detrital components). Lithofacies 2 represents the clay-bearing intervals in the Wyandot Formation and record an increase in the quantity of clay minerals (mostly kaolinite) and detrital material delivered to the ocean floor (although detrital material still has low percentage volumes; <5% quartz from point counting). Some of the clay minerals are authigenic in origin (discussed in more detail below) but some of the argillaceous and detrital content could be terrigenous in origin, probably air-born, as it indicated by the silt-sized quartz (Wetzel, 1984). Lithofacies 2 is interpreted to have been deposited either in intervals of lower productivity than lithofacies 1 when the background siliciclastic sedimentation was less diluted by carbonate production, or during times of increased terrigenous input, or a combination.

4.6. Ichnofabric-based core descriptions

4.6.1. Eagle D-21

Eagle D-21 recovered 26 m of core from depths of 1639 m to 1665 m. Lithofacies 1 (chalk) dominates the well with thin, <5 cm thick, beds of lithofacies 2 (Fig. 4.5). Eagle

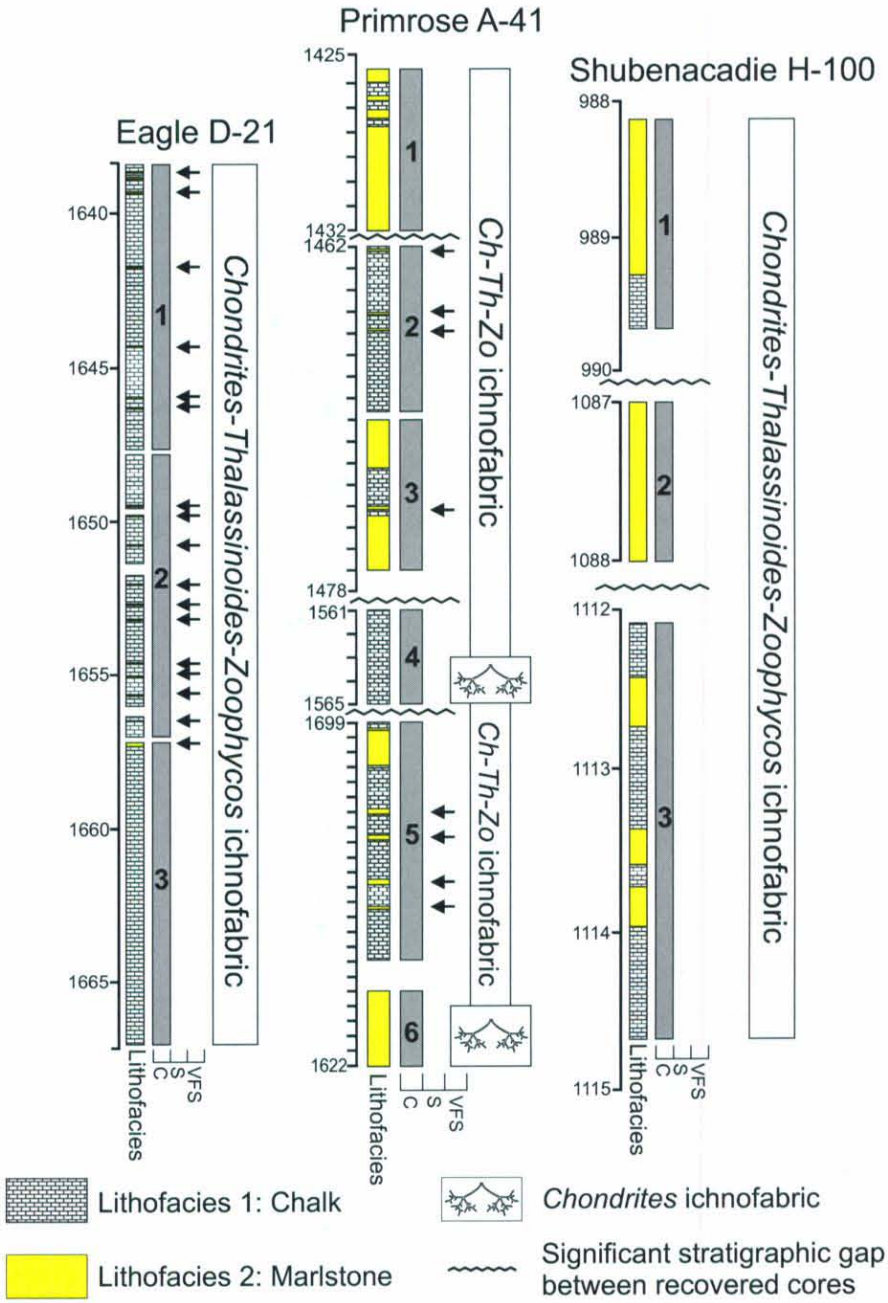
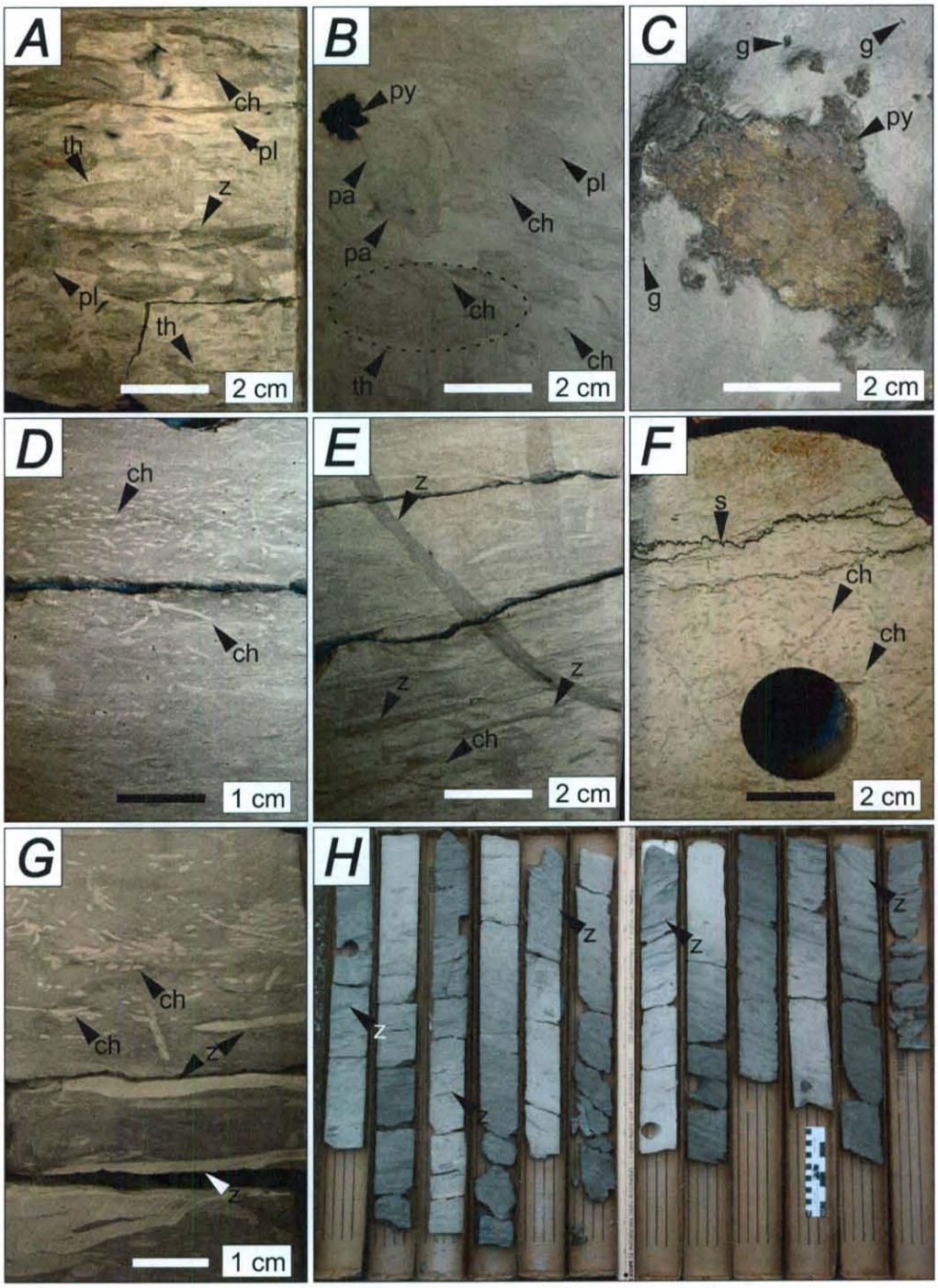


Fig. 4.5. Graphic logs of the studied well drilled through the Wyandot Formation (not drawn to the same scale). The *Chondrites-Thalassinoides-Zoophycos* ichnofabric (abbreviated to *Ch-Th-Zo*) dominates all cored intervals. Brief changes to the *Chondrites* ichnofabric are rare (labelled). Arrows indicate the presence of thin beds of lithofacies 2. Numbered columns refer to the core number from each well. Scale bars are in metres. C, claystone; S, siltstone; VFS, very fine sandstone.

D-21 is bioturbated by a *Chondrites-Thalassinoides-Zoophycos* ichnofabric (Plate 4.3A-B). This ichnofabric is formed by high densities and high abundances of *Thalassinoides* commonly overprinted by *Zoophycos* (Plate 4.3A). *Chondrites* overprint all ichnogenera indicating they were emplaced last in the sediment (Plate 4.3B). Accessory trace fossils include *Palaeophycus* and *Planolites* (Plate 4.3B). Both of these ichnogenera are shallow tier trace fossils found in the oxygenated sediment of the mixed layer close to the sediment-water interface (Pemberton & Frey, 1982). As a result *Palaeophycus* and *Planolites* are commonly reworked by mixed layer and deeper-burrowing animals so are not volumetrically abundant in the Wyandot Formation. Abundances of *Chondrites*, *Thalassinoides*, and *Zoophycos* vary but this is considered to be due to the patchy nature of trace fossils in core and the narrow width of core giving a limited perspective of the depositional environment at a particular stratigraphic level. The *Chondrites-Thalassinoides-Zoophycos* ichnofabric shows no change in trace fossil dimensions (ichnometry) or in trace fossil assemblage (ichnodiversity) throughout Eagle D-21 (Fig. 4.5; Plate 4.3). These observational data along with high bioturbation indices (BI 5-6) imply that the mixed layer was completely bioturbated by shallow burrowing and near-surface benthos. Ichnofabric analysis implies a well-oxygenated sediment-water interface and stable palaeoenvironmental conditions during deposition of the Wyandot Formation in the locality of Eagle D-21.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4.6.2. Primrose A-41

The base of the well (near the contact between the Wyandot Formation and underlying Dawson Canyon Formation) has abundant authigenic pyrite and glauconite. Nodules of pyrite up to 4 cm across are seen in association with glauconite grains less than 1 mm wide (Plate 4.3C). *Chondrites* is the only ichnogenus associated with these mineral-bearing horizons, forming a 4 m thick interval of a *Chondrites* ichnofabric (1622 m to 1618 m on Fig. 4.5; Plate 4.3D). The presence of authigenic minerals coupled with the low ichnodiversity imply reducing pore water conditions, probably resulting from an upward migration of the redox boundary due to either (1) lowered bottom water oxygenation (Bromley & Ekdale, 1984; Savrda & Bottjer, 1986), or (2) an increase in organic matter delivered to the sediment (Gehlen *et al.* 1997; Wetzel, 2010). Lowered oxygenation at the sediment-water interface and within the substrate would elicit a concomitant response from the benthic community (i.e. a decrease in trace fossil size, diversity, abundance, and a decrease in the penetration depth; see Table 5 in Wetzel, 1991). Low ichnodiversity is observed; however, there is no decrease in *Chondrites* burrow dimensions compared to *Chondrites* preserved in ichnofabrics from well-oxygenated settings. Likewise, the bioturbation index remains high (BI 5-6) indicating the mixed layer was bioturbated, removing primary sedimentary fabric, and implying no significant decrease in bottom water/pore water oxygenation at the sediment-water interface (Reimers *et al.* 1986). Lowered oxygenation is therefore inconsistent with our observations. An increase in organic matter delivered to the seafloor can result in lowered pore water oxygenation and anoxia in bathyal areas (Wetzel, 2010). Oxygen is

metabolized by microbial reactions during the remineralization of organic carbon, increasing the redox boundary in the sediment and water column, leading to pore water anoxia (Gehlen *et al.* 1997). This is observed in many modern deep-ocean settings (e.g. the South China Sea; Wetzel, 2002, 2008). The unknown *Chondrites* constructor is suggested to have had a chemosymbiotic relationship with sulphur-oxidizing bacteria therefore able to metabolize organic matter using H_2S formed from the reduction of sulfate (Seilacher, 1990; Fu, 1991). Consequently, the deep-burrowing *Chondrites* tracemaker would have been tolerant to this inferred increase in sedimented organic matter and the ensuing lowered pore water oxygenation. *Chondrites*-dominated ichnofabrics can be interpreted to represent environmental perturbations affecting the endobenthic community. At stratigraphically higher levels in the core (1618 m to 1565 m on Fig. 4.6) there is a decrease in the abundance of authigenic minerals and an increase in the diversity and abundance of ichnogenera (Plate 4.3E). The *Chondrites-Thalassinoides-Zoophycos* ichnofabric was described from this section of core. This suggests environmental conditions suitable for benthic life with higher respiratory needs without possible chemoautotrophic symbionts. This interval of ameliorated conditions is interrupted by a 2 m thick succession (1565 m to 1563 m on Fig. 4.6) of heavily stylolitized chalk where the *Chondrites*-dominated ichnofabric is observed (Plate 4.3F). This change in ichnofabric implies another sedimented organic matter increase which led to the exclusion of other ichnogenera. The *Chondrites* ichnofabric is replaced by the *Chondrites-Thalassinoides-Zoophycos* ichnofabric at 1563 m and continues to the top of the well at 1425.5 m (Fig. 4.5). The increase in ichnodiversity, abundance, and density of bioturbation implies a return to more equable conditions probably related to a lowering of

the redox boundary allowing penetrative sediment exploration by an increased number of endofauna. Deep-burrowing endobenthic communities can be supported by sediment organic matter contents of 0.2-0.4% C_{org}, inferred by comparison with modern day pelagic setting (Wetzel, 1984). Increases in the argillaceous content in the upper part of the cored interval are associated with high densities of bioturbation by *Zoophycos* tracemakers (Plate 4.3D, G). Modern examples of *Zoophycos* are found in such sediments, preferring clay- and silt-grade sediments (Wetzel & Werner, 1981; Wetzel, 1983). This could account for the high abundance of Wyandot *Zoophycos* in the muddier sections of the well (see below; Plate 4.3H).

4.6.3. Shubenacadie H-100

The Shubenacadie well is dominated by the *Chondrites-Thalassinoides-Zoophycos* ichnofabric (Plate 4.3H). Shubenacadie H-100 proved challenging to study as constant wetting of the core's surface has caused expansion of clay minerals (mostly kaolinite) and a flaky surface texture. The Wyandot Formation becomes more argillaceous at stratigraphically higher intervals (Fig. 4.5). This caused a problem for identification finding smaller ichnogenera such as *Chondrites*, which are apparently absent in the more argillaceous intervals of Shubenacadie H-100. The Shubenacadie H-100 well recovered both lithofacies 1 and 2 (chalk and marlstone, respectively) with no accompanying change in ichnofabric (Fig. 4.5; Plate 4.3H). The Shubenacadie well is consistently and highly bioturbated (BI 5-6) by *Chondrites*, *Thalassinoides*, and *Zoophycos* from 988.2 m to 1114.6 m, the length of the cored interval with subsidiary *Palaeophycus* and *Planolites*

(Fig. 4.5). *Zoophycos* is the most volumetrically dominant trace fossil and was the last trace fossil to be emplaced in this ichnofabric (as it overprints all ichnogenera; Plate 4.3H). *Zoophycos* tracemakers can burrow up to 1.5 m beneath the seafloor (Håkansson *et al.* 1974), below the redox boundary (Wetzel, 1983). The abundance of feeding burrows such as *Zoophycos* have been considered to indicate lowered oxygen (Ekdale & Mason, 1988) in pore waters at depth in the sediment but should not be taken as evidence for lowered bottom water oxygen levels, especially when the depth of bioturbation cannot be established (see Wetzel, 1991). The *Chondrites-Thalassinoides-Zoophycos* ichnofabric suggests that there was little to no significant change in palaeoenvironmental conditions throughout this depositional interval and evidenced by the unchanging benthos as there is no significant variations in ichnofabric, ichnometry, or ichnodiversity noted. This suggests a well-oxygenated sediment-water interface and no environmental perturbations.

4.7. Biological effects on the texture of fine-grained sediment

Bioturbation changes the physical and chemical properties of sediments, especially in slowly accumulated pelagic successions, where most sediment grains were probably processed multiple times by burrowing organisms (Ekdale & Bromley, 1984). This is illustrated in the Wyandot Formation by the high bioturbation indices (BI 5-6) and mottled fabrics (Figs 4.4-4.5; Plate 4.2). Burrowing organisms have the potential to change the chemistry of their surroundings through bioirrigation (pumping of seawater

into pore waters) and biodeposition (deposition of faecal matter on or within the sediment; Aller, 1982; Herringshaw *et al.* 2010). Bioirrigation and biodeposition alter the biogeochemical microenvironment in the substrate making burrows and faecal pellets the loci for the early diagenetic processes that effect reservoir quality (Gingras *et al.* 1999, 2007).

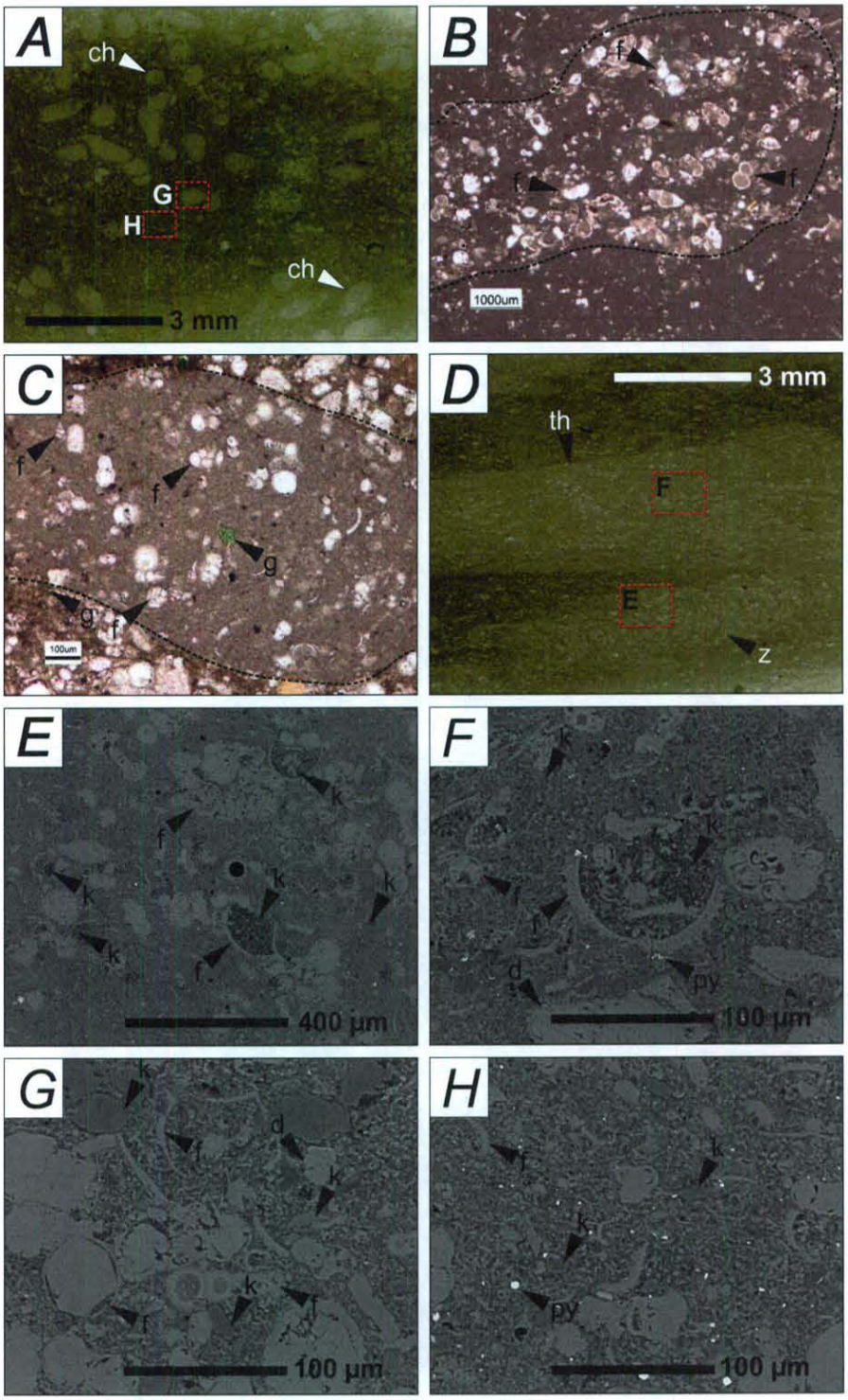
Endobenthic organisms cause physical disruption of sedimentary laminae and the redistribution of sedimentary particles (Berger & Heath, 1968; Goldring, 1995; Herringshaw *et al.* 2010). This bioturbation changes the primary sediment porosity and permeability of the substrate, which can impact upon the reservoir potential and the flow of hydrocarbons through reservoir facies (Gingras *et al.* 2007). Biogenically enhanced permeability can improve reservoir quality with burrow-controlled flow paths for fluids and can improve connectivity between reservoirs (Gingras *et al.* 1999; Pemberton & Gingras, 2005). Alternatively, endobenthic organisms can decrease the permeability and porosity of the host sediment by packing fine-grained material into their burrow walls (Tonkin *et al.* 2010). As endobenthic organisms move through and feed on the substrate they can introduce significant heterogeneity to the sediment. Mineralogical heterogeneities can be introduced by organisms egesting sediment of a different mineralogical composition to the host sediment (McIlroy *et al.* 2003). This is of particular importance in reservoir facies as the introduction of a significant volume of fine-grained material can impede hydrocarbon flow and reservoir quality (Gingras *et al.* 2007). The effect of bioturbation on sediment texture and composition was therefore investigated in the Wyandot Formation.

4.7.1. Burrow fill vs. ambient sediment

Selected thin sections were analysed under SEM to examine the mineralogy and texture of chalk and marlstone and their relation to biological structures. Thin sections containing *Chondrites*, *Planolites*, *Thalassinoides*, and *Zoophycos* were studied. Apart from the spreiten-burrow *Zoophycos*, all burrow fills were found to be homogeneously foraminifer-rich. *Zoophycos* burrows show alternating coccolith-rich and foraminifer-rich spreite (Plate 4.4A).

4.7.1.1. Foraminifers

The burrow fills of *Chondrites*, *Planolites*, and *Thalassinoides* are coccolith-dominated and contain abundant foraminifer tests and test fragments (Plate 4.4B-C). The greatest concentration of foraminifers is within burrows (Plate 4.4B). Point counting revealed that burrow fills comprise 30-70% foraminifer by volume, with ambient sediment containing 10-60% by volume (an 86% enrichment of foraminifers in burrow fills; Fig. 4.4; Plates 4.2 & 4.4B-C). The increases in foraminifer density in burrow fills could indicate that the trace-making organisms were feeding directly upon foraminifers (cf. Sliter, 1971), deposit feeding on foraminifer-rich sediment, or that the passively-filled *Thalassinoides* and *Zoophycos* burrows were rich in winnowed foraminifers. The foraminifer-rich burrow fill of *Planolites* (Plate 4.4B) was probably a result of either direct deposit feeding or scavenging as the *Planolites* is actively filled by the burrowing animal (Pemberton & Frey, 1992). Active collection of foraminifers by macrofauna has previously been documented where burrows are filled with agglutinated protozoans scavenged from the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sediment surface (Kaminski & Wetzel, 2004). The tracemakers of *Planolites* and *Thalassinoides* in the Wyandot Formation may similarly represent predation on protistans. Within the burrow fills, many foraminifer chambers are cemented with calcite (Fig. 4.4E; Plates 4.2G & 4.4E, G), whilst foraminifer in the host sediment are generally uncemented (Fig. 4.4F). The chamber-filling cement may be derived from recrystallization of foraminifer tests or the coccolith-rich matrix. *Zoophycos* spreiten are composed of back-filled bands of tightly packed foraminifer test fragments and coccoliths (Plate 4.4D-E).

4.7.1.2. Clay minerals and pyrite

Kaolinite is the most abundant clay mineral identified in burrow fills of the Wyandot Formation (Plates 4.2F-G & 4.4F). Burrow fills of *Chondrites*, *Planolites*, and *Thalassinoides* were found to contain up to 40% kaolinite, compared with up to 30% in some lithofacies (percentages obtained from point counting; Plate 4.4G-H). This equates to a 33% enrichment of clay minerals (kaolinite) in the burrows fills relative to the host sediment. Other clay minerals were found in very low abundances (<5%) in burrow fills and include smectite group minerals and chlorite. These accessory minerals were identified on EDS spectra by their high peaks for Al and Si with minor peaks for K, Ca, Fe, and Mg, in conjunction with their high birefringence when the same thin sections are studied using optical microscopy. This combination of characters identifies the clays as smectite group clay minerals (Odom, 1984; Deer *et al.* 1992). The host sediments are coccolith- and foraminifer-rich but have a less diverse and abundant clay mineral assemblage restricted to variable amounts of kaolinite (amount dependent on lithofacies;

Fig. 4.4; Plates 4.2 & 4.4H). Pyrite framboids are equally distributed in burrow fills and host sediment implying that the burrowing organisms had little, if any, control on the sulphur and iron chemistry of the sediment during framboid growth. Burrows that would have been open to the sediment-water interface and possibly actively ventilated (e.g. *Chondrites* and *Thalassinoides*) might be expected to have a decreased abundance of pyrite around oxygenated burrow margins. This was not observed.

4.7.1.3. Biological weathering

Optical and SEM petrography of the Wyandot Formation has shown that clay mineral assemblages are more diverse and that clay minerals are more abundant in burrow fills than in the host sediment (Fig. 4.4; Plates 4.2 & 4.4). The concentration of fine-grained material in burrow fills probably represents a feeding strategy, since organic carbon is often associated with clay mineral surfaces in fine-grained sediments (Wetzel, 1991) and adsorbed onto the more surface-rich fraction of the sediment (Lopez & Levinton, 1987). Some of the differences in clay mineral distribution could also result from biological weathering of sedimentary grains (cf. McIlroy *et al.* 2003). Deposit feeding on clay mineral-rich sediment can lead to clay mineral authigenesis, breakdown, and transformation within the digestive system of endobenthos (McIlroy *et al.* 2003; Needham *et al.* 2005). The preferential accumulation of clay minerals such as chlorite group minerals, kaolinite, and smectite group minerals in the burrow fills of the Wyandot Formation is probably the result of selective deposit feeding and authigenic alteration of ingested clay minerals in the reducing microenvironment of a deposit feeder's foregut (cf. McIlroy *et al.* 2003; Needham *et al.* 2004, 2005). Deposit feeding can thus concentrate

clay minerals in burrow fills via selective feeding and/or biological weathering. Faecal burrow fills are thus typically enriched in diagenetically reactive clay minerals relative to the cleaner, less mineralogically diverse host sediment. The low volumes of clay minerals in the host sediment of the Wyandot Formation (particularly in lithofacies 1) could suggest that the kaolinite found in burrow fills is mostly authigenic/biogenic in origin. This is supported by observational data that shows irregular euhedral and "books" of kaolinite crystals filling foraminifer chambers within burrow fills when studied under SEM (Plates 4.2F & 4.4E-F). This indicates that the burrow-filling kaolinite grew post-depositionally. The effects of textural heterogeneity on reservoirs as a result of deposit feeding and biodeposition is under-studied with few papers published (McIlroy *et al.* 2003; Pemberton & Gingras, 2005; Tonkin *et al.* 2010). This process is of particular importance when one considers that bulk sediment feeding endobenthos can introduce significant amounts of fine-grained material and clay minerals into the sediment by biodeposition. Consequently, endofauna in the Wyandot Formation have the potential to significantly reduce reservoir quality by introducing heterogeneity into chemically and texturally pure chalks (lithofacies 1).

4.8. Conclusion

The Wyandot Formation is thick carbonate reservoir facies preserving primary porosities of up to 35% (Ings *et al.* 2005) with an oil and gas discovery in the Primrose N-50 well and a gas discovery in the Eagle D-21 well (Wielens *et al.* 2002; Ings *et al.* 2005).

Assessing the possible distribution of, and controls upon the porosity and permeability in this unit is thus as an important component of assessing the Wyandot as a possible reservoir unit. The Wyandot Formation contains a trace fossil assemblage comparable to many coeval deep-water chalk deposits (Bromley & Ekdale, 1984; Savrda & Bottjer, 1989; Locklair & Savrda, 1998). Ichnofabric analysis presented herein has shown that the depositional environment of the Wyandot Formation was relatively stable during the deposition of the recovered wells. The *Chondrites-Thalassinoides-Zoophycos* ichnofabric dominates most of the recovered wells with only two environmental perturbations interpreted by the appearance of the *Chondrites* ichnofabric (Fig. 4.4; Plate 4.4). *Chondrites*-dominated ichnofabrics are conventionally considered as indicators of lowered oxygen levels at the sediment-water interface (Bromley & Ekdale, 1984; Savrda & Bottjer, 1986; Uchman, 2004). In the Wyandot Formation the low bottom water oxygen model is inconsistent with observations as there is no decrease in the size of *Chondrites* and the background chalk is highly bioturbated (BI 5-6). We interpret the Wyandot Formation *Chondrites* ichnofabric as being related to increases in sedimented organic matter leading to enhanced microbial remineralization and an upward shift of the redox front (Wetzel, 2010). The resulting dysoxic sediment precluded all but the trace maker of *Chondrites*, which is widely considered to be highly tolerant of a range of physiological stresses. Influxes of organic matter may have been seasonal but there is limited objective evidence for this preserved in the chalks as intense bioturbation (BI 5-6) has removed all primary sedimentary fabrics including bedding. Trace fossil analysis has shown that the Wyandot Formation was entirely deposited under softground conditions.

No firmgrounds were discovered indicating an absence of erosion and no significant depositional hiatuses associated with seafloor diagenesis.

Petrographic analysis of the formation indicates that it is dominantly comprised of productivity-derived material from the photic zone. Coccoliths and foraminifer are the dominant component of both lithofacies (Fig. 4.4; Plate 4.2). The kaolinite-bearing host sediment of lithofacies 2 is interpreted to have been deposited during periods when primary productivity lessened or terrestrial input increased. The only detrital clay mineral found in the host sediment is kaolinite with an increased abundance of clay minerals seen in burrow fills. *Chondrites*, *Planolites*, *Thalassinoides*, and *Zoophycos* burrows contain kaolinite along with smectite group minerals and chlorite-group clay minerals identified from SEM image analysis. The increase in clay mineral abundance and diversity in burrow fills is here inferred to be the result of clay mineral alteration and low temperature authigenesis as a result of passage through the reducing microenvironment of an organism's foregut (cf. McIlroy *et al.* 2003). Low volumes of clay minerals in lithofacies 1 suggest that the increase in clay mineral content of burrow fills is probably authigenic/biogenic in origin.

This study highlights some drawbacks associated with highly bioturbated pelagic deposits. Under low sediment accumulation rates endobenthos can remove all primary sedimentary fabric resulting in a preserved fabric dominated by biogenic structures (trace fossils) and homogenized sediment. Continual overprinting of trace fossil tiers means no colonization surfaces can be observed. Thin event beds may also be removed from the geologic record by this continual sediment churning by the endobenthic community. This paper also highlights the implications for unfavourable reservoir heterogeneity that can be

introduced by burrowing organisms. Large-scale biodeposition may significantly alter the texture of fine-grained sediments and consequently fluid migration paths and reservoir properties.

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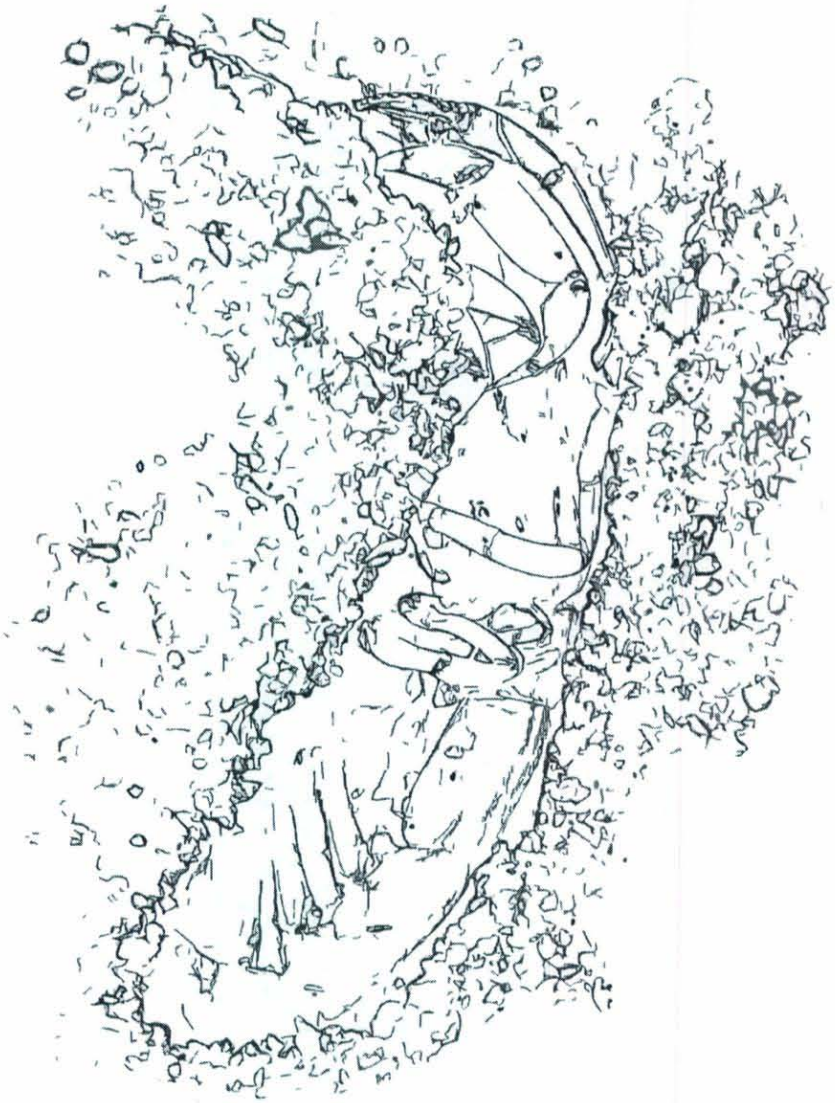
CHAPTER 5

Contributions to the ichnology and ichnofabrics of deep marine settings: discussion and conclusions



CHAPTER 5

Contributions to the ichnology and ichnofabrics of deep marine settings: discussion and conclusions

5.1. Introduction

This thesis demonstrates the utility of trace fossil analysis and the ichnofabric method in delineating environmental changes using two sedimentological end-member systems (rapid episodic deposition in the Grès d'Annot Basin, SE France, and continuous pelagic deposition in the Wyandot Formation, offshore Nova Scotia). In addition, using field observations from the Grès d'Annot Basin a neoichnological study is presented that provides an explanation for one of the most common styles of endobenthic colonization in turbidite settings. The aim of this research is to improve the applicability of trace fossil analysis in the identification of depositional environments and environmental stresses through changes in palaeo-benthic communities. The preceding chapters show, independently and cumulatively, that trace fossil analysis is an important tool for sedimentologists, petroleum geologists, and other workers interested in producing depositional models, making palaeoenvironmental reconstructions, and elucidating ancient tracemaker behaviour.

5.2. Research conclusions

5.2.1. Chapter 2: the response of benthic organisms to event bed deposition

The Grès d'Annot Basin, SE France, is an ideal natural laboratory for studying trace fossil assemblages associated with turbidity current deposition. With a sedimentological and stratigraphic framework already in place (Sinclair, 1997; Apps *et al.* 2004; Callec, 2004; Stanbrook & Clark, 2004) the response of benthic organisms to environmental disturbance could be successfully assessed. Fieldwork consisted of bed-by-bed logging and sampling of turbidite system components in the Marnes Brunes Inférieures and Grès d'Annot Formations. The trace fossil assemblages and ichnofabrics of the Grès d'Annot Basin had been hitherto unstudied.

Turbidite ichnology has been studied in many basins worldwide (Uchman, 1995, 1998, 2001; Heard & Pickering, 2008) but rarely using the ichnofabric method, which can provide more detailed description and has the resolution to document bed-by-bed changes in trace fossil assemblages (Knaust, 2009). Good exposure in the Grès d'Annot Basin allows for the description of thick stratigraphic successions encompassing many different facies that comprise typical turbidite systems. Ichnological differences in pre- and post-depositional assemblages were identified in different palaeoenvironments from intra-basin slopes to the basin floor. The main results of this field study are:

1. The Grès d'Annot Basin is a thrust sheet-top basin with a complex topography at the time of turbidite deposition. Consequently, there is a suppression of distal and

thin-bedded facies which are intrinsic to the preservation of near-surface grazers, shallow deposit feeders, traps and farming structures. As a result, the turbidites of the Grès d'Annot Basin preserve mainly deep-burrows made by tracemakers adapted to living deep in the sediment (e.g. *Ophiomorpha* and *Thalassinoides*).

2. Turbidite successions in the Grès d'Annot Basin are characterized by low diversity and high abundance assemblages, dominated by the crustacean burrow *Ophiomorpha rudis*. The palaeoenvironmental implications for *Ophiomorpha rudis* are addressed fully in Chapter 3.
3. Thin-bedded and distal turbidites of the Marnes Brunes Inférieures Formation are characterized by a largely vagile; mostly deposit feeding community of endobenthic organisms with a greater preservation for pre-depositional trace fossil assemblages (Plate 2.4). These assemblages are found on the soles of distal turbidites and hemipelagic deposits on intra-basin slopes or in areas of thin-bedded channel fill facies as a result of channel abandonment. These settings were characterized by a higher trace fossil diversity and more complex ichnofabrics than settings dominated by more erosive and higher power turbidity current events (Fig. 2.3). Heterolithic and mud-dominated facies have higher ichnodiversity and higher bioturbation indices (commonly homogenized by burrowing organisms; BI 5-6) than sand-dominated facies in the Grès d'Annot Basin.
4. Pre-event trace fossil assemblages found in association with thin-bedded turbidites include *Asterosoma*, *Ophiomorpha annulata*, *O. rudis*, *Paleodictyon*, *Planolites*, and *Scolicia*. This ichnological assemblage is indicative of quiescent

palaeoenvironmental conditions punctuated by low power turbidite currents (Plate 2.4).

5. Ichnofabrics such as the *Ophiomorpha annulata – Planolites* ichnofabric and the *Phycosiphon – Ophiomorpha rudis* ichnofabric are preserved and are characteristic of the low current energy settings of intra-basin slopes and channel fill facies (Figs 2.3 & 2.5-2.9). The diversity of ichnofauna, dominance of shallow-burrowing and near-surface trace, and lack of significant deep-burrowing suggests that these ichnofabrics characterizes a well-oxygenated sediment-water interface with no significant nutrient stress.
6. Palaeoenvironments characterized by episodic, high current energy conditions are found in channelized and turbidite proximal fan settings in the Grès d'Annot Formation (Figs 2.4-2.5). The sand-dominated facies found in these settings have low bioturbation indices (BI 0-1) and a low diversity trace fossil assemblage restricted to large, penetrative burrows constructed by deep-burrowing crustaceans (*Ophiomorpha rudis* and *Thalassinoides suevicus*).
7. Ichnofabrics documented from channelized and proximal fan settings belong to the *Ophiomorpha rudis* ichnofabric association. *Ophiomorpha rudis* dominates the ichnofabrics in these settings seen penetrating multiple turbidite beds and thick turbidite sandstone, up to 2 m thick, before ramifying into horizontal galleries at sandstone-mudstone interfaces (Plate 2.3F & Plate 2.4C, E, respectively). This burrowing behaviour represents a nutritional strategy in the aftermath of turbidity current events when endobenthic organisms were forced to burrow into the

sediment to find nutrition (burrowing behaviour explored in more detail in Chapter 3).

This paper is the first detailed ichnofabric study of Grès d'Annot turbidite system and one of the first systematic studies of turbidite ichnofabrics in the field (cf. Wetzel & Uchman, 2001). This study is a comprehensive ichnological analysis of one of the most important turbidite depositional system (cf. Joseph & Lomas (eds) 2004). Remarkably, the Grès d'Annot Basin had not previously received focussed ichnological consideration. The data acquired in the course of this thesis demonstrates that trace fossil analysis is an effective tool in delineating environmental stresses (in this case, nutrient stress) and that trace fossils and ichnofabrics can be used to define depositional environments in deep-water turbidite systems. This work in the Grès d'Annot Basin has shown that endobenthic animals construct distinct burrow types as adaptations to substrate type, oxygenation, organic matter content, grain-size, and hydrodynamic energy. In thick-bedded turbidites, only deep burrows are seen while fine-grained, thin-bedded facies are preferentially colonized by shallow and surface grazers such as echinoderms and polychaetes (Wetzel, 1984). The lower diversity compared to other turbidite systems (Crimes, 1973; Crimes *et al.* 1981; Uchman, 1995, 1998, 2001; Heard & Pickering, 2008) is probably due to the confined nature of the Grès d'Annot Basin and its position as a thrust sheet-top basin causing deposition of sand-rich, highly erosive turbidity currents. The paucity of thin-bedded and distal turbidites is considered to account for the low diversity of trace fossils (especially graphoglyptids) relative to unconfined turbidite fan systems (cf. Uchman, 2001).

5.2.3. Chapter 3: a new model for trace fossil distribution at sandstone-mudstone junctions in turbidite systems

The work in the Grès d'Annot Basin presented in this thesis has shown that trace fossils, particularly *Ophiomorpha rudis* and *Thalassinoides suevicus*, are found in high abundances on sandstone turbidite soles and at sandstone-mudstone interfaces (Plate 2.1H; Fig. 3.1A; Phillips *et al.* 2011). This distribution was the most commonly observed taphonomic expression of *Ophiomorpha* and *Thalassinoides* throughout the Grès d'Annot Basin and has also been noted by authors from other turbidite systems worldwide (Uchman, 1995, 1998). At present, this distribution of ichnotaxa in has hitherto been unexplained, despite being a common observation in many field studies (Uchman, 1995, 1998, 2001; Heard & Pickering, 2008). Mesocosm experiments were constructed to see if progenitors of *Ophiomorpha* and *Thalassinoides* have a preferential distribution relative to buried sand-mud interfaces and to ascertain what are the controls on any burrow distribution observed? Many authors have speculated on a possible link between deep-burrowing endofauna and microbial farming (MacGinitie, 1978; Miller, 1984; Uchman, 2009). This paper uses mesocosm experiments, CT imagery, and geochemical data to propose a solid link between burrow distribution and microbial farming in deep marine systems. Our mesocosm experiments were carried out at Memorial University in a laboratory with marine aquaria. The thalassinid crustacean *Neotrypaea californiensis* was used a modern analogue for the ancient tracemaker of *Ophiomorpha rudis*. *Neotrypaea californiensis* is a shallow-water and intertidal mud shrimp which can be collected relatively easily and has been used in many field and laboratory experiments (Thompson

& Pritchard, 1969; Miller & Curran, 2001). A Toshiba Xpress/GX medical CT scanner was used to map the distribution burrows constructed in the aquaria. The ichnologically modified sediment in the tanks was then sampled for geochemical analysis, also carried out at Memorial University.

1. *Neotrypaea californiensis* constructed a pelletal burrow wall morphologically similar to the trace fossil *Ophiomorpha rudis* (i.e. a partially lined roof with discoid muddy pellets; Plate 3.1D-E; Uchman, 2009). Colonization of the sediment by *N. californiensis* was through vertical burrowing activity down through sand and then horizontally along sand-mud interfaces in the mesocosm setups (Plate 3.1D-F).
2. Tanks were mapped in three dimensions using computed axial tomography to produce a three-dimensional reconstruction of the burrow system beneath the sediment (Fig. 3.4A-B). The shrimps followed sand-mud interfaces producing burrow distributions that are morphologically similar to ancient *Ophiomorpha* and *Thalassinoides* observed in the Grès d'Annot Formation and other turbidite systems (see Chapter 2; Plates 2.1E-H & 2.2F-G; Uchman, 1995, 1998).
3. After the burrow-lining pellets had been constructed *Neotrypaea californiensis* was observed to feed from the pellets. *Neotrypaea californiensis* picked at a single pellet each feeding time passing sedimentary particles over its mouth, probably ingesting the most organic carbon-enriched grains in the pellets. The geochemistry of the mesocosm and burrow-lining sediment was investigated using total organic carbon (TOC) and stable isotope analyses.

4. Geochemical analysis revealed that samples taken from *Neotrypaea californiensis* burrow walls had higher TOC values compared to unbioturbated material taken from the same mesocosm (Fig. 3.5A). These higher values are probably the result of *N. californiensis* selecting organic-rich grains to place into the burrow walls and pellets. This sieving activity was observed in the mesocosms during wall pellet production. The organic carbon-enriched pellets became sites of higher microbial productivity (indicated with stable isotope analysis) producing dissolved organic carbon (DOC) acting as a nutritional resource for the burrowing shrimp.
5. $\delta^{13}C_{org}$ data shows a uniform grouping of values in the unbioturbated samples from the host sediment (Fig. 3.5B). The $\delta^{13}C_{org}$ signature obtained from the burrow walls and pellets is heavier relative to the unbioturbated material sampled from the sample mesocosm (Fig. 3.5B). This indicates isotopic fractionation in the walls which is probably the result of aerobic microbial productivity in the organic carbon-enriched pellets. Microbial respiratory processes preferentially use the lighter ^{12}C isotope which has subsequently been released into the water column enriching the pellets in the heavier ^{13}C. Isotopically lighter samples are considered to indicate enrichment of ^{12}C by increased microbial biomass and DOC probably due to anaerobic microbial fractionation (sulphate-reducing or methanogenesis).
6. It is concluded that *Neotrypaea californiensis* (and by extension the tracemakers of ancient *Ophiomorpha* and *Thalassinoides*), at least facultatively, farmed microbes in the pellets that lined their burrow walls, especially when the pellets were produced in a sandy substrate. By bioirrigating their burrows *N.*

californiensis provided a suitable geochemical microenvironment within its burrow walls to allow microbial colonization of the pellets. By maintaining an oxygenated burrow at the interface between sand and organic carbon-rich mud, the shrimp encourage a large microbial community producing a stockpile of DOC to meet its nutritional requirements.

7. This paper demonstrates a nutritional strategy which allows the production of labile DOC from refractory detrital organic matter in deep marine sediments. This adaptation is common in shallow-water thalassinids and might constitute a pre-adaptation to life in deep marine sediments which commonly have abundant, but refractory, organic matter buried at depth.

The published literature on geochemistry and its relationship to bioturbation originate from studies in intertidal or shallow-water settings (Aller, 1978; D'Andrea *et al.* 2002, 2004). This is the first study to combine field and laboratory observations, CT imagery, and geochemical data to provide a link between trace fossil distribution and tracemaker ethology in deep marine systems. Fig. 5.1 shows the relationship between TOC in turbidite successions and bioturbation. Bioirrigation increases the oxygen flux into the sediment (Zorn *et al.* 2006) providing microbial communities with oxygen and, in conjunction with organic carbon commonly found in buried inter-turbidite mud, provide microenvironments for high microbial productivity. This productivity results in higher TOC values in the sediment areas surrounding bioirrigated burrows. The buried interface between sand and mud in turbidite deposits is pump-primed for exploitation by deep-burrowing infauna. By bioirrigating, the progenitors of interface trace fosils such as

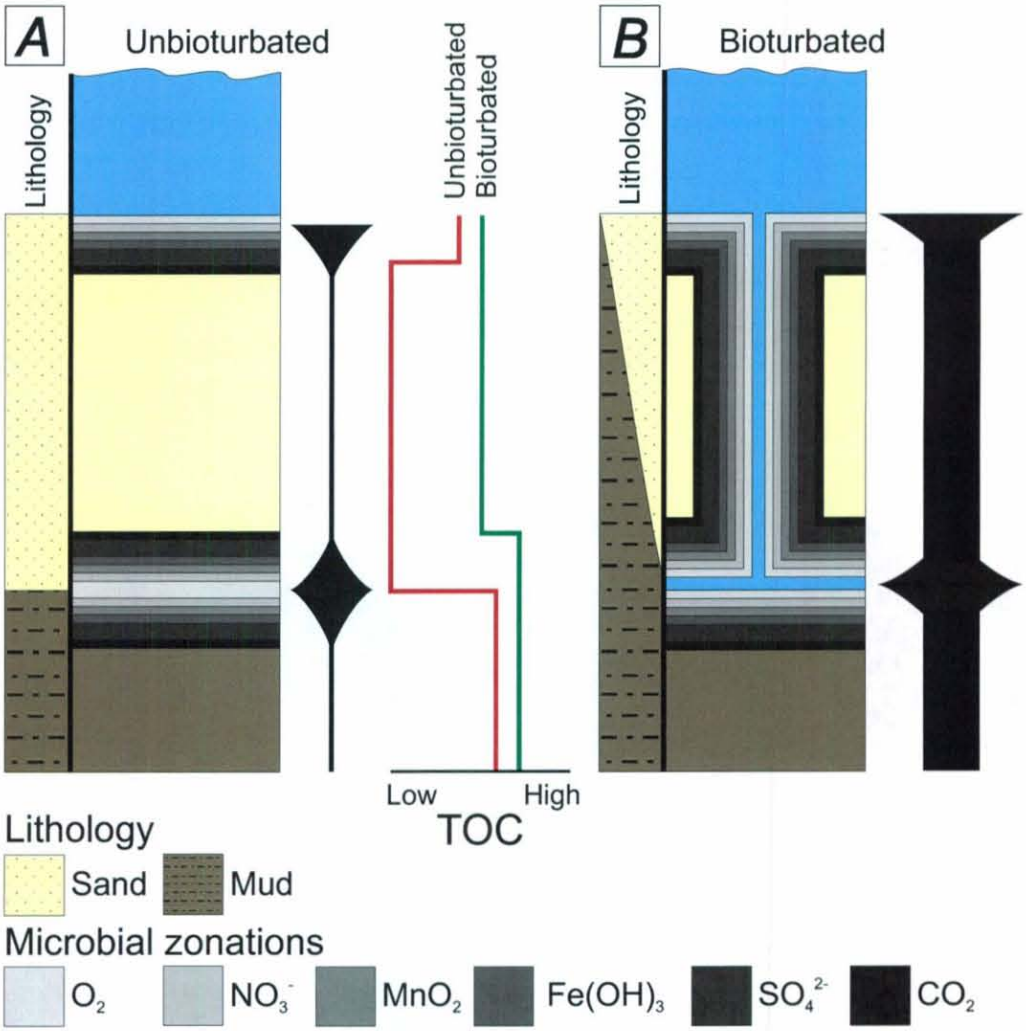


Fig. 5.1. Pump-priming of a hypothetical turbidite sedimentary system for deep-sediment miners. The black lines alongside each sedimentary column show an increase or decrease in microbial productivity through the succession. **A.** No bioturbation (mud horizon produces an oxidant-limited microbial system as oxygen (from the newly deposited sand) is used in microbial respiration at the interface between the oxygenated sand and the organic-rich mud. Microbial productivity is temporarily high at the interface. **B.** A bioturbated turbidite. Oxygen is pumped into the sediment resulting in an increased oxygen flux and higher microbial productivity compared to unbioturbated strata. The gradual change from mud to sand in the lithology column demonstrates the incorporation of sand into the muddy roof pellets constructed by *Neotrypaea Californiensis* and introduced to the entire sand body. The middle column incorporates the geochemical data from the mesocosms and show that TOC content of the sediment would be higher in the bioturbated turbidite due to increased, and continual, aerobic respiration and remineralization of organic carbon during the lifetime of the bioirrigated burrow. Diagrams modified from Aller (1982).

Ophiomorpha and *Thalassinoides* can maintain this high microbial productivity and farm microbes at depth in the sediment. This paper provides a model for the patterns of *Ophiomorpha* and *Thalassinoides* seen in deep-water and turbidite settings in basins worldwide related to a deep-sediment farming strategy.

5.2.3. Chapter 4: high resolution ichnofabric analysis of pelagic deposition and clay mineral alterations

The Upper Cretaceous Wyandot Formation, offshore Nova Scotia is an autochthonous carbonate composed of chalk and interbedded marlstone. The Wyandot Formation is recovered from three wells drilled on the Scotian Shelf (see Fig. 4.2 for locations). These wells are the Eagle-D21, Primrose A-41, and Shubenacadie H-100. Split cores drilled through the Wyandot Formation were examined at the Canada-Nova Scotia Offshore Petroleum Board, Dartmouth, Nova Scotia. The Wyandot Formation was used to examine how palaeoenvironmental changes affect endobenthic organisms in pelagic sediment and how high resolution ichnofabric analysis can be used to identify environmental perturbations in the rock record. Petrographic analysis revealed biologically mediated changes in the texture and mineralogy of these deposits. The main conclusions of this paper are:

1. The Wyandot Formation can be divided into two autochthonous lithofacies which are both dominated by the products of primary production. These lithofacies are: (1) a bioturbated, foraminifer- and coccolith-rich, calcareous claystone (chalk;

Fig. 4.4), and (2) a bioturbated, foraminifer- and coccolith-rich, kaolinite-bearing, calcareous claystone (marlstone; Plate 4.2). These descriptions follow the classification scheme for fine-grained sediments defined by Macquaker & Adams (2003).

2. The Wyandot Formation carbonates are intensely bioturbated with all primary sedimentary structures removed in the mixed layer (BI 5-6). Ichnogenera described from the Wyandot Formation include *Chondrites*, *Palaeophycus*, *Planolites*, *Teichichnus*, *Thalassinoides*, and *Zoophycos* which have been documented from coeval chalk and marlstone deposits worldwide (Plate 4.1; Ekdale & Bromley, 1983, 1984; Locklair & Savrda, 1998a, 1998b).
3. A *Chondrites-Thalassinoides-Zoophycos* ichnofabric characterizes the vast majority of the recovered cores drilled through the Wyandot Formation (Fig. 4.5; Plate 4.3). The eponymous ichnogenera are found in high densities and abundances in the ichnofabric. *Chondrites*, *Thalassinoides*, and *Zoophycos* all maintain an open (and permanent) connection to the water column. Consequently, the *Chondrites-Thalassinoides-Zoophycos* ichnofabric is indicative of long, stable periods on the deep seafloor with a well-oxygenated sediment-water interface. There is no evidence for deposition of thick event beds.
4. Monogeneric *Chondrites* ichnofabrics represent the only ichnofabric variability documented from the Wyandot Formation (Fig. 4.5; Plate 4.3). Primary sedimentary fabrics are not preserved in the *Chondrites* ichnofabrics as they have a burrow-homogenized background (BI 5). This suggests that there was no decrease in oxygenation at the sediment-water interface as the mixed layer was

highly bioturbated; contrary to the traditional low oxygenation interpretation of *Chondrites*-only ichnofaunal assemblages (Savrda & Bottjer, 1986; Ekdale & Mason, 1988). Increases in sedimented organic matter are interpreted to result in *Chondrites* ichnofabrics. Porewater anoxia can result from increases in organic matter input into the sediment, causing rapid use of free oxygen by aerobic microbial respiration and a rising of the redox boundary in the sediment (Reimers *et al.* 1986; Wetzel, 2010). The *Chondrites* tracemaker with its inferred chemo-symbionts had a competitive advantage in low oxygen environments which exclude other deep-burrowing tracemakers (Bromley & Ekdale, 1984; Savrda & Bottjer, 1986).

5. Petrographic analysis of the Wyandot Formation has shown that bioturbation can change the texture and mineralogy of sediment. Foraminifer tests and test fragments were found to be 86% enriched in the burrow fills of *Chondrites*, *Planolites*, and *Thalassinoides* compared to the host sediment (Plate 4.4). The progenitors of these trace fossils were most likely deposit feeding on the foraminifer, concentrating them in burrow fills (cf. Sliter, 1971).
6. Kaolinite was identified as the most abundant clay mineral within the Wyandot Formation (identified by its low back scattered electron coefficient and diagnostic 1:1 ratio of Al to Si in EDS spectra; Deer *et al.* 1992). Burrow fills were found to contain up to 40% kaolinite compared to 30% in the ambient sediment (percentages obtained by point counting and dependent on lithofacies; Plate 4.4). Burrow fills are thus 33% more enrichment in kaolinite than the surrounding sediment.

7. The enrichment of clay minerals (principally kaolinite) in burrow fills relative to the host sediment implies that some of the clay mineral assemblages of burrow fills are authigenic. Booklets of kaolinite filling foraminifer chambers and large euhedral kaolinite crystals in the burrow fills indicate that these crystals are not detrital but formed as a result of biological weathering (Plate 4.4; cf. McIlroy *et al.* 2003). Deposit feeding endobenthos ingest clay minerals, and via low temperature authigenesis in the acidic microenvironment of the organism's digestive system, egest faecal material of a different mineralogy (Needham *et al.* 2004, 2005).

This paper illustrates the utility of ichnofabric analysis in the palaeoenvironmental interpretation in pelagic settings. Trace fossils are *in situ* records of environmental stresses. Changes in depositional conditions (i.e. increases in sedimented organic matter) elicit a change in the benthic community. In the Wyandot Formation the physiological stress on the biological community, and the ichnocoenoses preserved, can be interpreted via perturbation from the *Chondrites-Thalassinoides-Zoophycos* ichnofabric to the *Chondrites* ichnofabric. The results of this paper show that changes in the trace fossil assemblages and ichnofabrics can identify periods of stress on the deep seafloor which could potentially be used as semi-regional markers in pelagic systems.

The Wyandot Formation has an oil and gas discovery in the Primrose A-50 well and a gas show in the Eagle D-21 well (Wielens *et al.* 2002; Ings *et al.* 2005). Other chalk reservoirs are sites of active petroleum production, particularly in the North Sea (Van der Bark & Thomas, 1980; Needham & Jacobs, 1995). The Eldfisk Field in the

Norwegian Central Trough, North Sea, is an active chalk reservoir (Brasher, 1995). The Eldfisk Field chalks are more favourable as a reservoir facies as they are mostly category III chalks (i.e. they are allochthonous) which preserve a greater porosity than category I chalks (Brasher & Vagle, 1996). The Wyandot Formation are autochthonous deposits made of category I chalks as defined by Brasher & Vagle (1996). This category, due to their slowly accumulated nature, tighter packing, and intense bioturbation make them less desirable as hydrocarbon exploration targets because of the accompanying reduction in porosity with burial (Brasher & Vagle, 1996).

Further to exploration, production petroleum geology is affected by bioturbation (Gingras *et al.* 1999, 2007; Pemberton & Gingras, 2005; Tonkin *et al.* 2010). The potential to introduce a significant amount of heterogeneity into reservoir facies by burrowing organisms is illustrated herein. Ingestion, passage through a reducing foregut, and egestion can change clay mineral assemblages and can have subsequently and significant implications for porosity and permeability. Biological weathering and clay mineral authigenesis can also introduce clay-grade material into sand-rich substrates, reducing the permeability, porosity, and reservoir quality of the sediment (Needham *et al.* 2005). This is of particular concern in type I chalk reservoirs, like the Wyandot Formation, which have already lost primary porosity by mechanical and chemical compaction (Brasher, 1995; Brasher & Vagle, 1996).

5.3. Discussion: deep-water ichnology

Trace fossils are *in situ* biological structures which record the environmental, sedimentological, and depositional conditions at the time of their construction. They have been used as palaeoenvironmental indicators, in stratigraphic studies, and deciphering physiologically stressful conditions in many ancient depositional systems (Crimes, 1977; Ekdale & Bromley, 1983, 1984; Ekdale & Mason, 1988; Wetzel, 1991; Uchman, 1995, 1998; McIlroy, 2004, 2007; Buatois *et al.* 2001, 2009; MacEachern *et al.* 2007a, 2007b, 2007c; Heard & Pickering, 2008; and in this thesis; see also Phillips & McIlroy, 2010; Phillips *et al.* 2011). Despite this abundance of literature, the application of trace fossil analysis has primarily focused on marginal and shallow marine systems (MacEachern *et al.* 1992a, 1992b; Pemberton *et al.* 1992, 2001; Martin & Pollard, 1996; McIlroy, 2004), with deep-water systems understudied in comparison. Likewise the ichnofabric method is rarely utilized in studies of turbidite systems (Knaust, 1998, 2009; Chapters 2 & 4 and Phillips & McIlroy, 2010; Phillips *et al.* 2011). This thesis makes a significant contribution, and highlights through a well-documented and well-studied field area how using a combined sedimentological and ichnological framework can lead to a better palaeoenvironmental reconstruction of ancient deep-water depositional systems. Ichnofabric analysis has been used in this thesis as a palaeoecological and palaeoenvironmental indicator of changing conditions in two end-member sedimentological systems in deep-water palaeoenvironments.

Palaeoenvironmental analysis uses trace fossil analysis to great effect (Pemberton *et al.* 2001; McIlroy, 2004, 2007; MacEachern *et al.* 2007c). This work has shown that to better understand ancient deep-water depositional systems, make more refined depositional models, and link ancient and modern settings trace fossil and ichnofabric analysis can be integrated with sedimentological facies analysis. Taking into account the biological factors, as well as the sedimentological, makes for higher resolution field- and core-based studies. Ichnofabric analysis can be used to decipher environmental change when there is a lack of primary sedimentary structures (e.g. in highly bioturbated settings; Chapter 4; Phillips & McIlroy, 2010). Enhanced palaeoenvironmental analysis is a significant tool used in petroleum geology, particularly in exploration geology (Martin & Pollard, 1996; McIlroy, 2004). In core-based work, trace fossils and ichnofabrics can be used as facies indicators, as well as indicators of depositional and environmental conditions (Chapter 2 & 4). The work done in the Grès d'Annot Basin is an example of this application (Chapter 2). Turbidite systems include a wide range of environments with differing styles of deposition (Pickering *et al.* 1989). Palaeoenvironmental analysis was carried out in the Grès d'Annot Formation using a combined ichnological and sedimentological approach. Trace fossil analysis and the ichnofabric method were successfully used to understand the depositional conditions controlling tracemaker behaviour, and from these data extrapolate the depositional palaeoenvironment within the turbidite system. This is more easily done in the field, as good exposure allows greater data collection to refine models, but the method employed in this thesis (Chapter 2) can be applied to core-based studies of turbidite systems.

Trace fossils can also be used to identify stressed conditions on the ancient seafloor (Bromley & Ekdale, 1984; Savrda & Bottjer, 1986; Uchman, 2004; MacEachern *et al.* 2007b). This thesis used trace fossil analysis to identify palaeoenvironmental stresses on the ancient seafloor by investigating stratigraphic changes in trace fossil assemblages (Chapters 2 & 4). Nutrient stress and oxygen stress where identified as the leading causes of ichnofabric variability and changes in trace fossil assembles in the Grès d'Annot Basin and Wyandot Formation, respectively (Chapter 2 & 4, respectively). This information is vital for reconstructing high resolution analyses and models to identify stresses affecting the benthic community that can be used in palaeoclimatic and palaeoceanographic studies.

Neoichnology is an expanding science with numerous studies using modern trace-making animals as analogues for ancient tracemakers (Miller & Curran, 2001; Gingras *et al.* 2008; Herringshaw *et al.* 2010). This paper showed that ancient tracemaker behaviour can be elucidated by neoichnological research. Using a modern progenitor, *Neotrypaea californiensis*, Chapter 3 provided a model for ancient burrows, like *Ophiomorpha rudis*, found in high abundance at sandstone-mudstone interfaces in turbidite systems. This research too, has significant implications for palaeoenvironmental analysis which can be used by other workers. This work allows us to refine the *Ophiomorpha rudis* ichnosubfacies of the *Nereites* ichnofacies erected by Uchman (2001). The *Ophiomorpha rudis* ichnosubfacies is currently used as an indicator of high current energy, proximal turbidite settings (Uchman, 2001, 2009). Field observations, presented herein, agree with this. For example, the *Ophiomorpha rudis* ichnofabric association documented form the Grès d'Annot Formation (Chapter 2) is seen in thick-bedded, coarse-grained turbidite

settings with high current energy, such as intra-channel areas and proximal fan systems. It is concluded from further research, presented in Chapter 3, that the distribution of *O. rudis* is not necessarily related to high energy currents but is found to be more closely linked the presence of buried nutrients. Consequently, the *Ophiomorpha rudis* ichnosubfacies (erected by Uchman (2001) and analogous to the *Ophiomorpha rudis* ichnofabric association in Chapter 2) can be refined to include not only sandy, high current energy settings, but areas where hemipelagic material in deeply buried by thick sands by turbidite deposition. This neoichnological research has demonstrated common tracemaker behaviour that can be used in other palaeoenvironmental studies in deep-water and turbidite systems. This new model can be used by other workers in ichnology, sedimentology, and petroleum geology as tool for better palaeoenvironmental reconstruction.

This thesis presents new data on deep-water ichnology and shows how ichnofabric analysis can be applied to deep marine palaeoenvironmental reconstructions. Three different approaches were used in this thesis to describe deep-water ichnology: (1) a field-based study in the Grès d'Annot Basin; (2) a core-based study on the Wyandot Formation, and; (3) a novel neoichnological approach to a hitherto unsolved paradigm. These three papers have shown that trace fossil and ichnofabric analysis have applications to studies in deep-water settings and can make a significant contribution to palaeoenvironmental analysis, when integrated with sedimentological facies analysis. This improved palaeoenvironmental analysis, facies characterization, and reservoir characterization has practical applications for petroleum geologists. The published work

arising from this thesis will be a first step towards making ichnological analysis in deep marine facies a routine and useful tool for petroleum geology and sedimentology.

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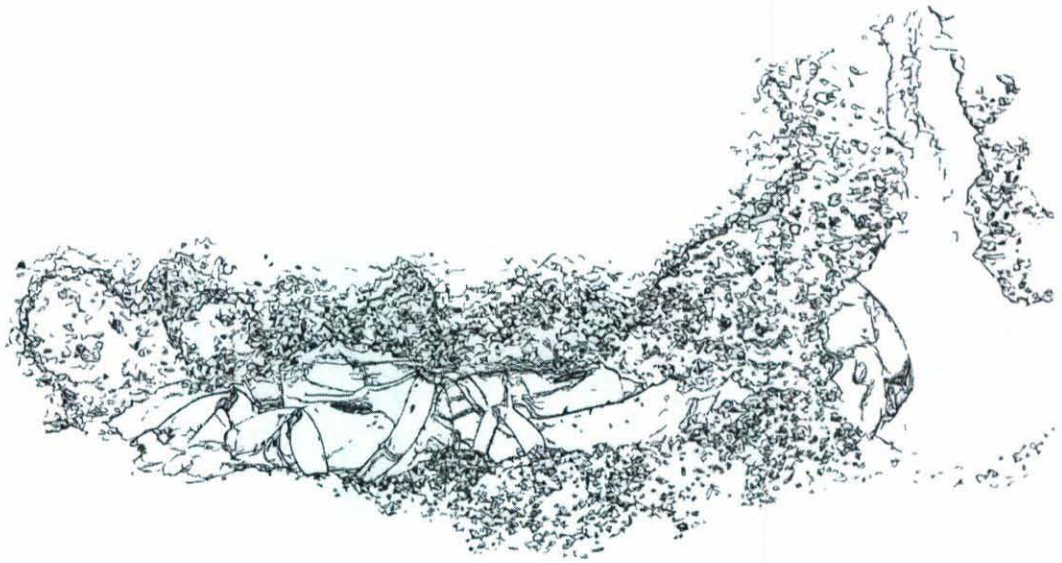
APPENDICES



APPENDIX A

Field logs and supplementary field images from the Grès d'Annot Basin, SE France

Explanation

This appendix is a compilation of logs and field images from the Grès d'Annot Basin. The purpose of Appendix A is to present some of the logs featured in Chapter 2 in more detail, at a larger scale, and with accompanying field images that were not included in the main body of this thesis. The following pages feature additional data from the Col de la Cayolle area with logs and images from Montagne de l'Avalanche, Tête Moulone, and Pra Giraud. The locations of these logs are shown in Figs 2.1 & 2.4-2.5.

The Col de la Cayolle outcrops are interpreted as an intra-channel palaeoenvironment with thickening- and coarsening-upwards packages of sandstone turbidites and little or no interbedded mudstone. A heterolithic succession of thin-bedded, fine-grained sandstone turbidites with interbedded siltstone and claystone lie conformably on top of this thick-bedded strata. This facies (facies 5) is interpreted as a change in the palaeoenvironment to channel abandonment with a concomitant reduction in current energy and an increase in the preservation of trace fossils (see Chapter 2). The logs from Montagne de l'Avalanche detail this channel abandonment facies. Tête Moulone logs are lateral equivalents of the channel abandonment facies whereas Pra Giraud outcrop thick-bedded and coarse-grained sandstone turbidites from intra-channel palaeoenvironment.

The log drawn from the Argenton onlap section was not shown in the previous chapters. It has the same sedimentary facies and trace fossil assemblages as other intra-basin slope settings documented in the Grès d'Annot Basin (see Figs 2.8-2.9 and the discussion in Chapter 2).

Legend

Below is the legend for all the logs presented on the following pages including lithologies, sedimentary structures, trace fossils, and macroscopic foraminifer species found in the Grès d'Annot Basin.

Lithology

Sandstone Siltstone Claystone No exposure

Sedimentary structures

Planar lamination Wavy lamination Convolute lamination Mudstone intraclasts

Trace fossils


Ophiomorpha


Thalassinoides

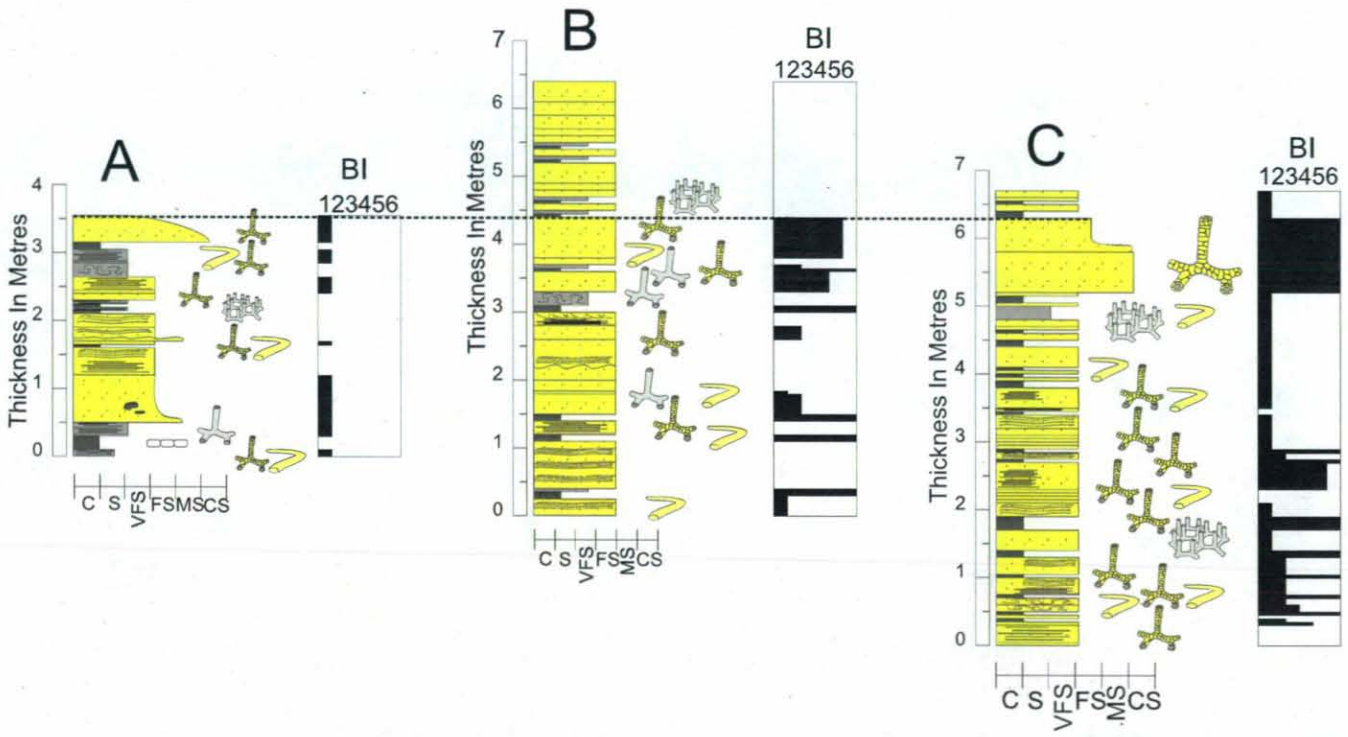

Paleodictyon


Planolites

Foraminifer

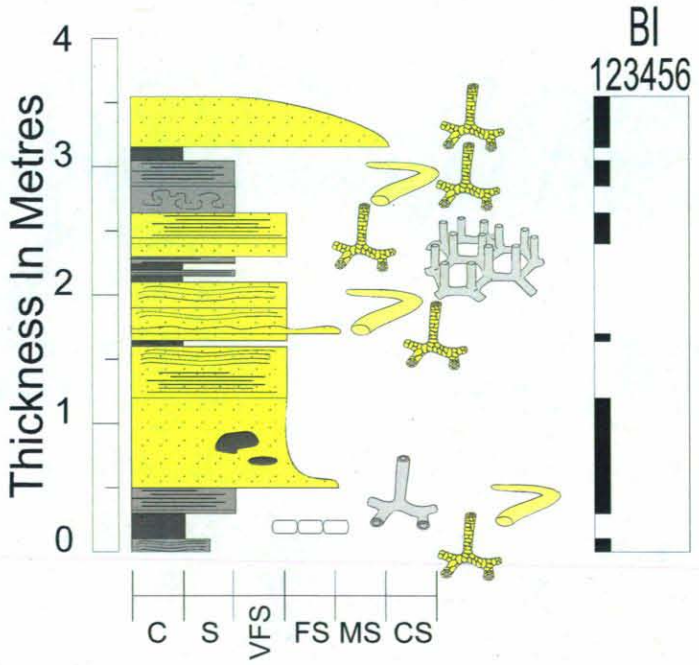

Bathysiphon

Montagne de l'Avalanche



Letters above logs correspond to the log positions are shown in Fig. 2.4 and Fig. 2.5A. Letters alongside the graphic logs on the following pages correspond to the field images on the following pages.

Montagne de l'Avalanche, log A



Very thick (2 cm) and long (>40 cm) *Ophiomorpha rudis*. Horizontal along a bed sole, mud lined.

Planolites in massive mudstone beds, thin-bedded.

Amalgamated sandstone beds with planar lamination. *Ophiomorpha rudis* 1.2 cm thick by 4 cm long with muddy pellets. Amalgamated beds with load structures and parallel lamination. Fine lag at base, massive bodies. No bioturbation.

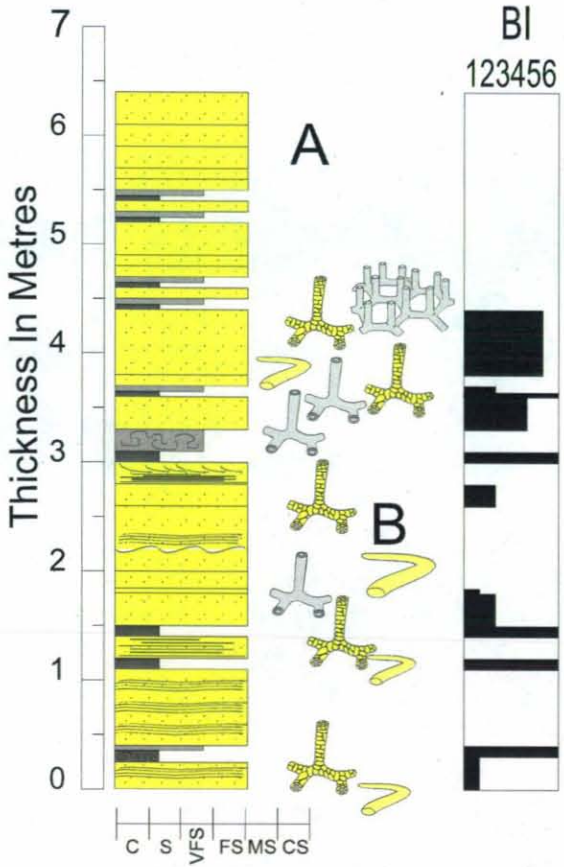
Ripple lamination on top, parallel, planar lamination in body. No

Very gentle grading. Intraclasts present, few still filled, most weatered out and hollow *Ophiomorpha rudis* only, emerging from a

Massive mudstone. No traces. *Bathysiphon*.

Parallel ripple lamination, Bouma Tcd. Ophiomorpha 1.5 cm thick by 5 cm long, pellets 3-5 mm diameter, mud-lined.

Montagne de l'Avalanche, log B



Thin-bedded sandstone and mudstone, 5-30 cm thick. No cyclicity. No bioturbation.

Highly bioturbated bed. Sandstone, massive. Vertical burrows, mud-lined. *Paleodictyon* seen in small patches on turbidite soles. *Thalassinoides* and *Ophiomorpha rudis* seen in massive sandstone beds.

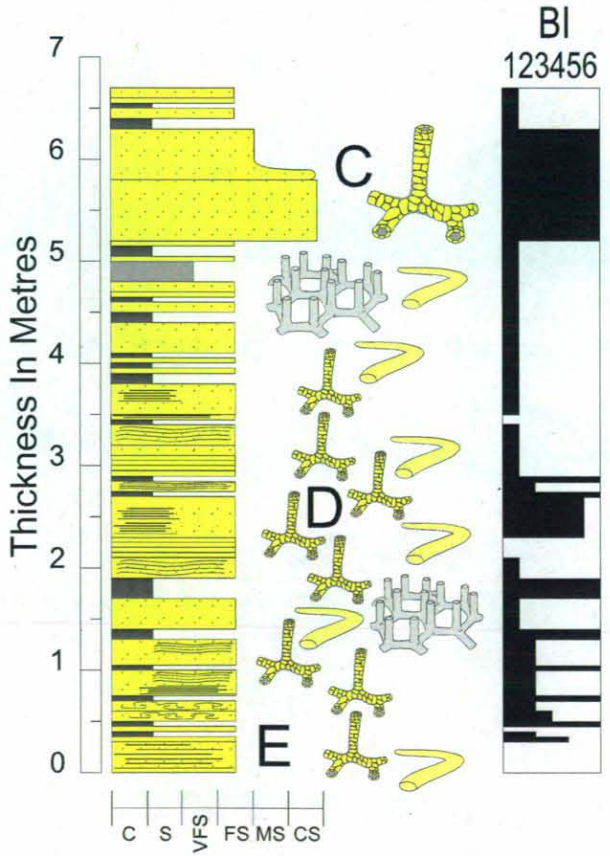
Convolute lamination.
Palaeocurrent to the north based on flute marks.
Backfilled structure - meniscate - mud-lined. Unusual *Ophiomorpha rudis*. See **Plate 2.4B** for image.
Massive sandstone beds, medium-bedded. Some beds show planar parallel lamination. Few traces, only *O. rudis*.

Bioturbated mudstone (massive) by *O. rudis*. Parallel lamination in sandstone.

Amalgamated beds with load structures and parallel lamination, ripple lamination. No bioturbation.

Parallel lamination in sandstone. *Ophiomorpha rudis*.

Montagne de l'Avalanche, log C



Thin-bedded sandstone and mudstone beds. Few trace fossils, only

Coarse-grained lag in sandstone bed. Lots of *O. rudis.*

Sandstone intensely mined by *Ophiomorpha*.

Thin-bedded sandstone and mudstone with *Planolites* and *Paleodictyon* on the soles of turbidite sandstone at sandstone-mudstone junctions.

Numerous sandstone beds with *Ophiomorpha* and *Planolites* burrows. Planar parallel and wavy lamination.

Sandstone beds with planar parallel, wavy, and convolute lamination. *Paleodictyon* on turbidite soles. *Ophiomorpha* and *Planolites* in sandstone and mudstone.

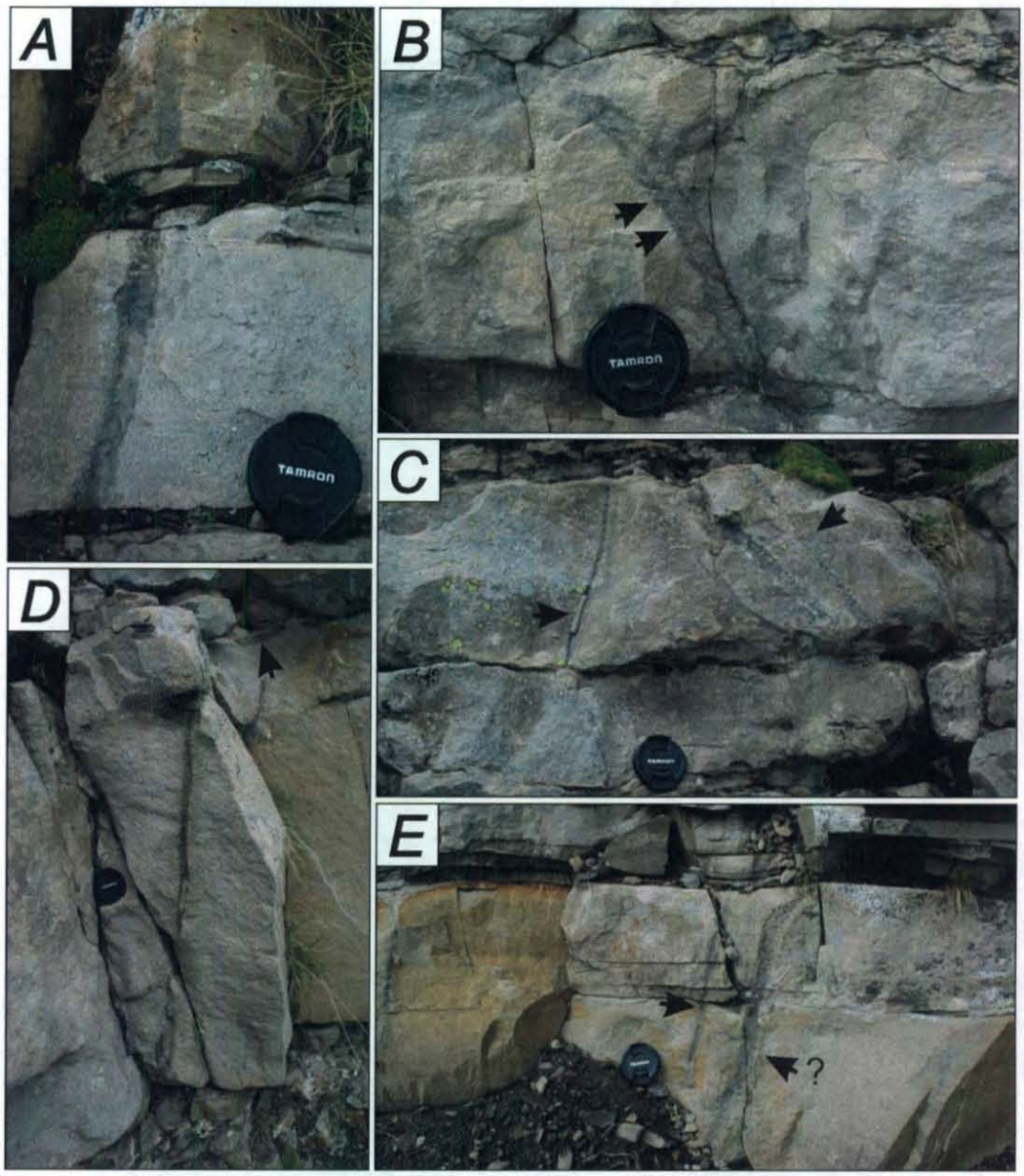
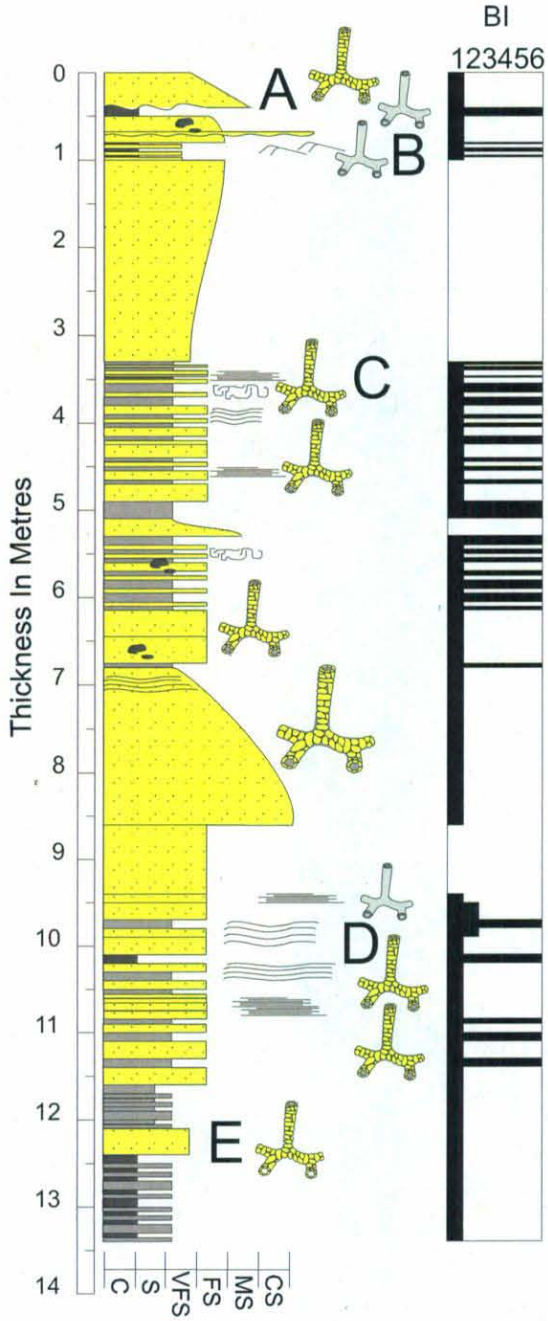


Fig. A1. Field images from the thin- and medium-bedded turbidites of facies 5, interpreted as channel abandonment facies. **A.** Vertical *Ophiomorpha rudis* with muddy pellets penetrating two thin-bedded sandstone turbidites. **B.** Sub-vertical *O. rudis* with a T-junction between and swelling. Note the muddy pellets on the external wall (arrowed). **C.** Several sub-vertical *O. rudis* of different sizes. A thin burrow penetrating two sandstone turbidites (left, arrowed) and a larger diameter, with large muddy pellets *O. rudis* (or possibly an *O.* ?*nodosa*; right, arrowed). **D.** Thin and vertical *O. rudis* penetrating a fine-grained, thin-bedded sandstone turbidite. The backfilled *O. rudis* (arrowed) is shown in more detail in Plate 2.4B). **E.** Vertical *O. rudis* (arrowed) and a possible *O. nodosa* (arrowed with a question mark) in a fine-grained sandstone turbidite. The lens cap is 5 cm wide.

Tête Moulone

This is an enlarged and detailed version of log D in Fig. 2.4. Log position is shown in the field image in Fig. 2.5B. Letters alongside the log indicate the stratigraphic positions of the field photographs shown in Fig. A2 on page A-9.



Numerous *Ophiomorpha*, horizontal, mud-lined. *Thalassinoides* , sub-horizontal, unlined in siltstone filled with siltstone.

No bioturbatoin. Coarsening upward sandstone bed.

Thin beds of siltstone and claystone bioturbated by *Ophiomorpha* only. Claystone is burrow homogenized whereas the siltstone has parallela and wavy lamination.

Thick sandstone turbidite. Fining upward with wavy lamination at the top, Bouma Tab. *Ophiomorpha* only. Seen to burrow down through the bed.

Massive sandstone with burrowed mudstone intraclast.

No bioturbation.

Interbedded sandstone and mudstone with wavy and parallel lamination. *Thalassinoides* (rare) and *Ophiomropha* only.

Heterolithic beds of sandstone and mudstone. *Ophiomorpha* only.

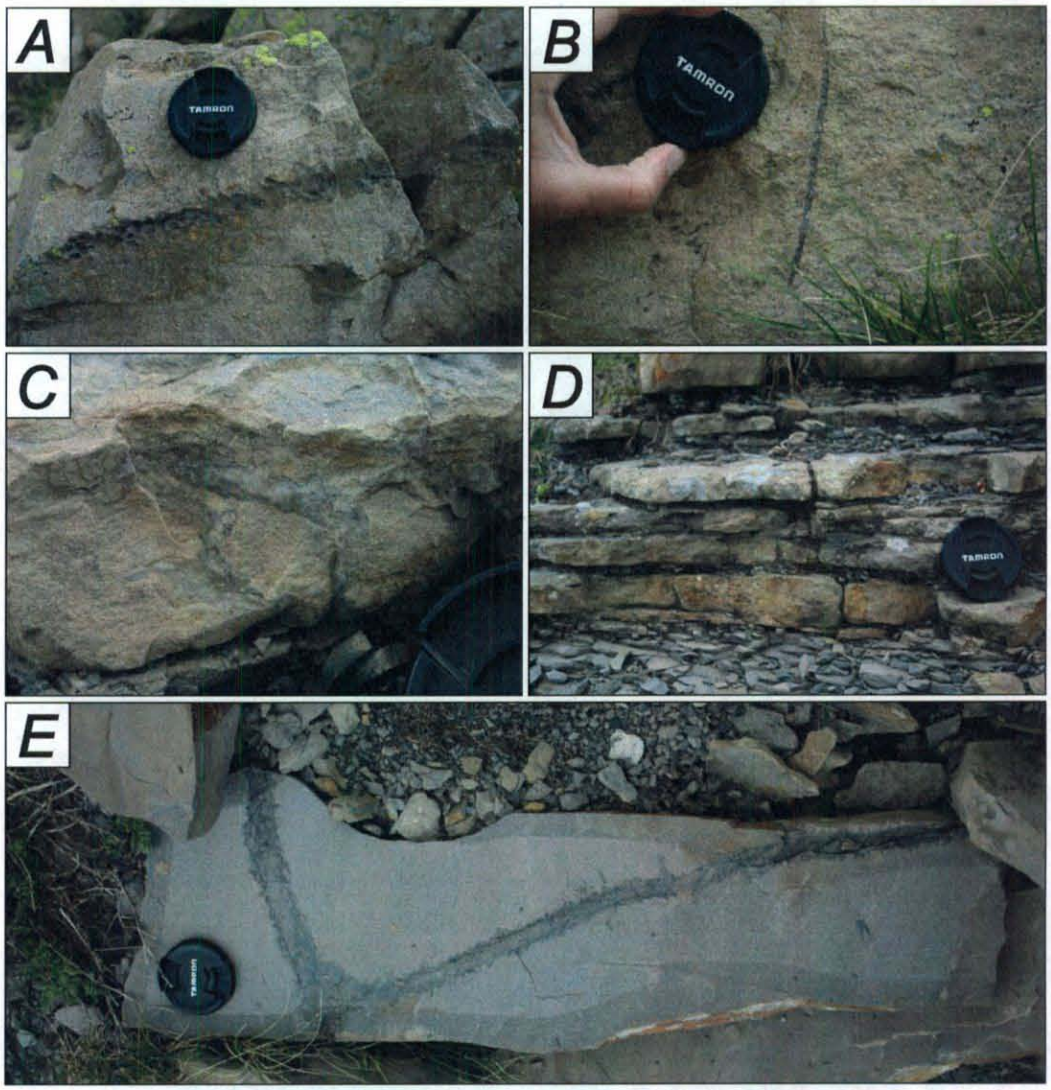
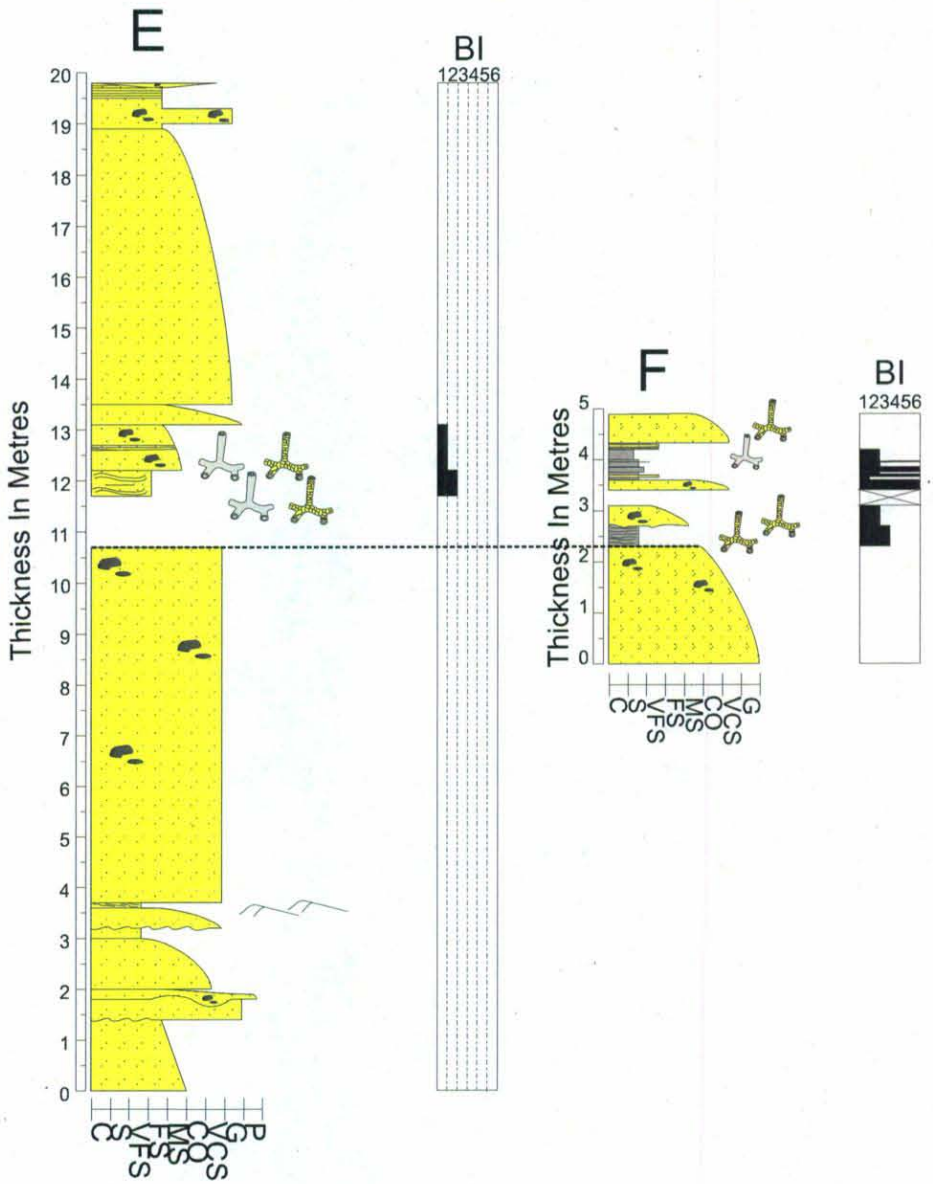


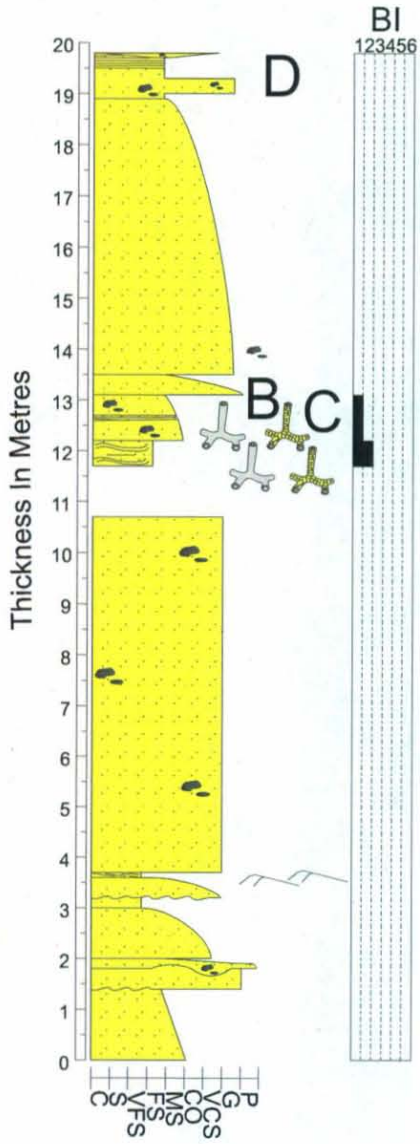
Fig. A2. Field images from Tête Moulone. **A.** Horizontal *Ophiomorpha rudis* with mud pellets in coarse-grained sandstone. **B.** Thin *O. rudis*, mud-lined. **C.** Mud-filled *O. rudis* on the sole of turbidites sandstone. **D.** Interbedded sandstone and mudstone. **E.** Large *O. rudis* with T-shaped bifurcations and swelling at the junction. Large mud pellets are arrowed. On float. The lens cap in 5 cm wide.

Pra Giraud



Letters above logs correspond to the log positions are shown in Fig. 2.4-2.5C.

Pra Giraud, log E



Medium-bedded sandstone with very coarse-grained scours. No bioturbation.

Coarse and very coarse-grained sandstone turbidites with no interbedded mudstone. Massive, normally graded with sandstone and mudstone intraclasts. No bioturbation.

Fining upward, coarse-grained sandstone turbidites. Vertical *Ophiomorpha*, sand-filled. Horizontal *Ophiomorpha* also seen. Filled with coarse sand. Presumed suspension feeding from active and waning current in intra-channel areas.

Very-coarse grained sandstone with pebbles and granules interspersed in the body of the turbidite, randomly orientated. Deposited from a high volume, high concentration turbidity current. No bioturbation.

More coarse-grained turbidites, Bouma T_{ab}. No bioturbaton.

Bouma T_{ab}. Normal grading.

Leters alongside the log correspond to field images on Fig. A3.

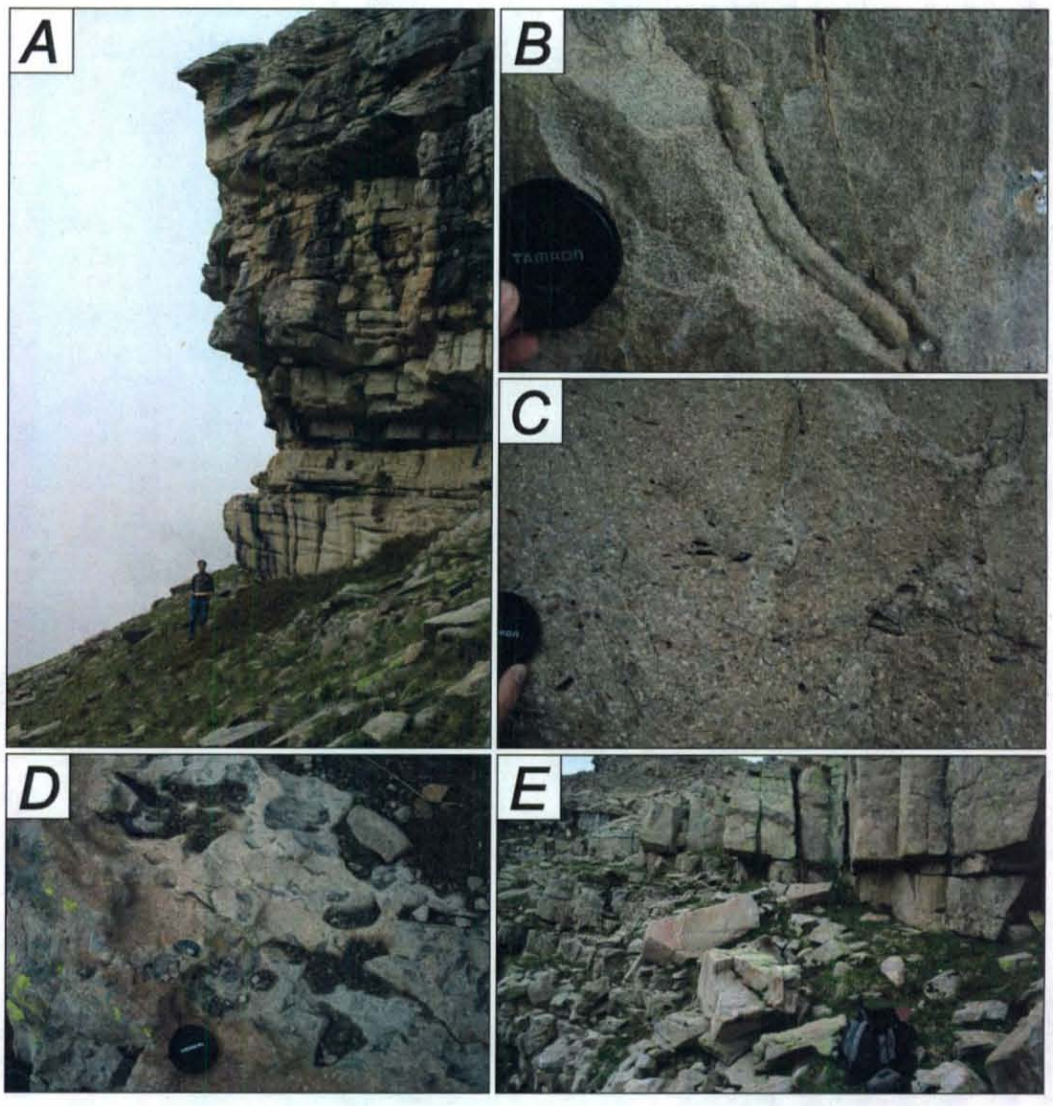
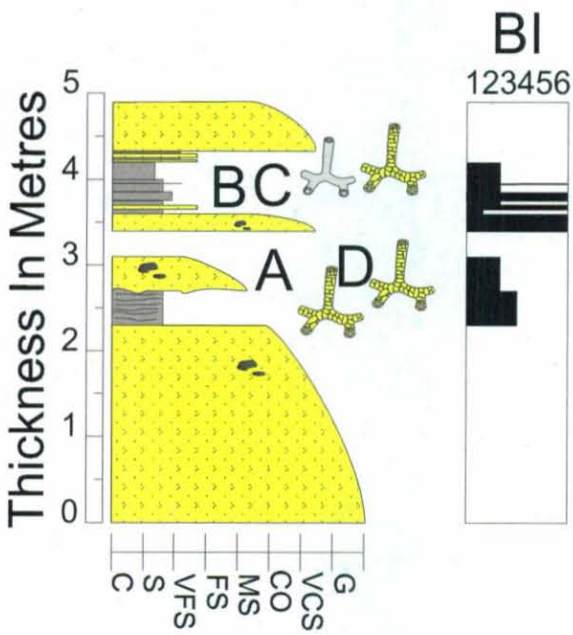


Fig. A3. Field images from Pra Giraud. **A.** Thick-bedded and amalgamated sandstone cliff at Pra Giraud. Field assistant for scale. **B.** *Ophiomorpha rudis* in a sandstone turbidite with sandy pellets (arrowed). **C.** Very coarse-grained sandstone with weathered out intraclasts. **D.** Top of a turbidite with large mudstone intraclasts, weathered out. **E.** Sandstone turbidites from the top of the outcrop drawn in log E.

Pra Giraud, log F



No bioturabtion.

Interbedded sandstone and mudstone. *Ophiomorpha*, mud-lined, small willed with sand.
Erosive contact. Mudstone intraclasts.

Ophiomorpha in siltstone filled with silstone.

Thick-bedded sandstone turbidite. Mudstone intraclasts at the top of the bed. Normal grading. No bioturbation.

Leters alongside the log correspond to field images on Fig. A4.

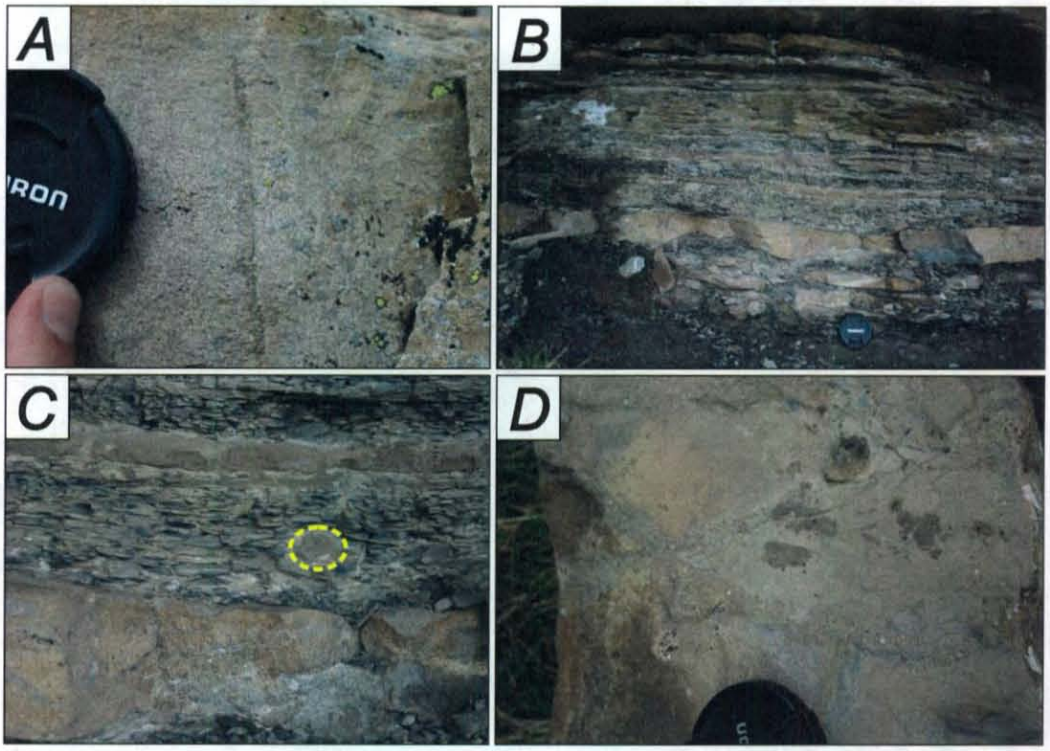
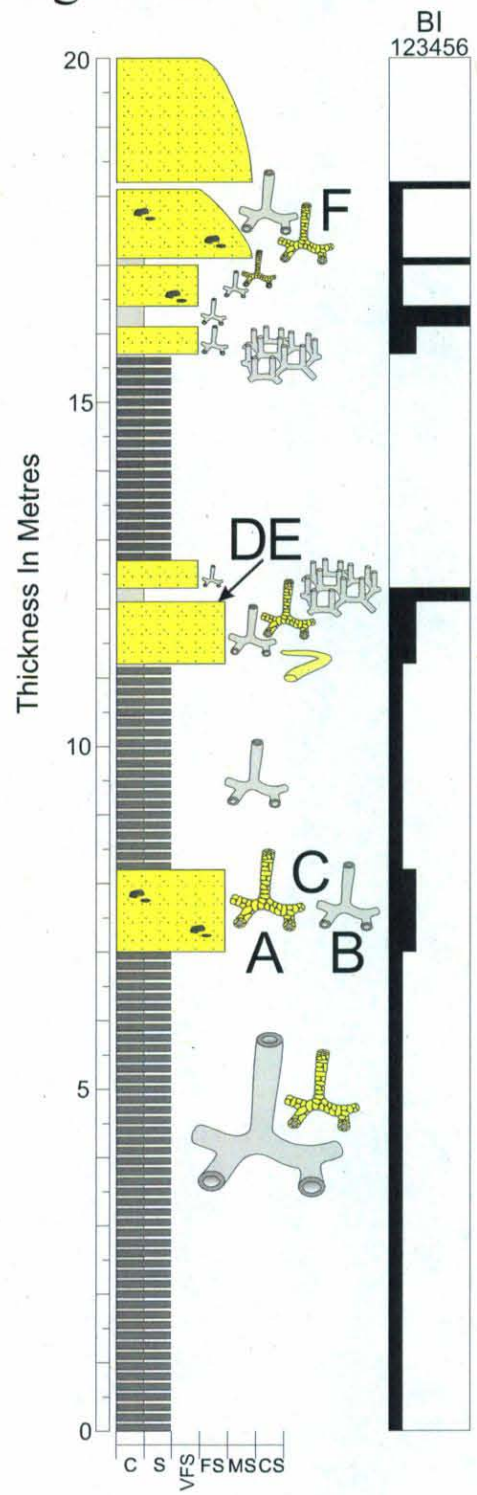


Fig. A4. Field images from log F. **A.** Thin, vertical *Ophiomorpha rudis* in sandstone. **B.** Interbedded sandstone and mudstone. **C.** Close up of heterolithic succession shown in **C.** *O. rudis* in cross-section in circled. **D.** *Ophiomorpha*/*Thalassinoides* filled with coarse-grained sandstone.

Argenton

Letters A-F alongside the log correspond to field images taken at that stratigraphic interval shown overleaf on Fig. A5.



Start of true Grès d'Annot Formation deposition. Thick-bedded sandstone turbidites with intraclasts (filled with siltstone). Horizontal and vertical *Ophiomorpha* and *Thalassinoides*. *Ophiomorpha* lined with sand or silt.

Thalassinoides (vertical) and *Paleodictyon* in sandstone.

No obvious trace fossils seen here. Unusual. More of the Marnes Brunes Inférieures Formation.

Massive sandstone. No bioturbation.
Massive clay
Massive sandstone. *Thalassinoides*, *Ophiomorpha, Planolites*, and *Paleodictyon* seen.

Interbedded brown and blue marls. More facies 6. *Thalassinoides* seen in very fine sandstone.

Massive sandstone turbidite with intraclasts, weathered out. This marks the start of deposition of the Grès d'Annot Formation. *Ophiomorpha* and *Thalassinoides* seen in this bed, heading down to and mining the intraclasts.

Thinly bedded silts (1-3 cm thick) and clays (1-10 cm thick) representative of facies 6 (see Chapter 2). Numerous fining-upward packages in rhythmic cycles. Marnes Brunes Inférieures Formation. Large *Thalassinoides* seen penetrating beds. Also *Ophiomorpha*.

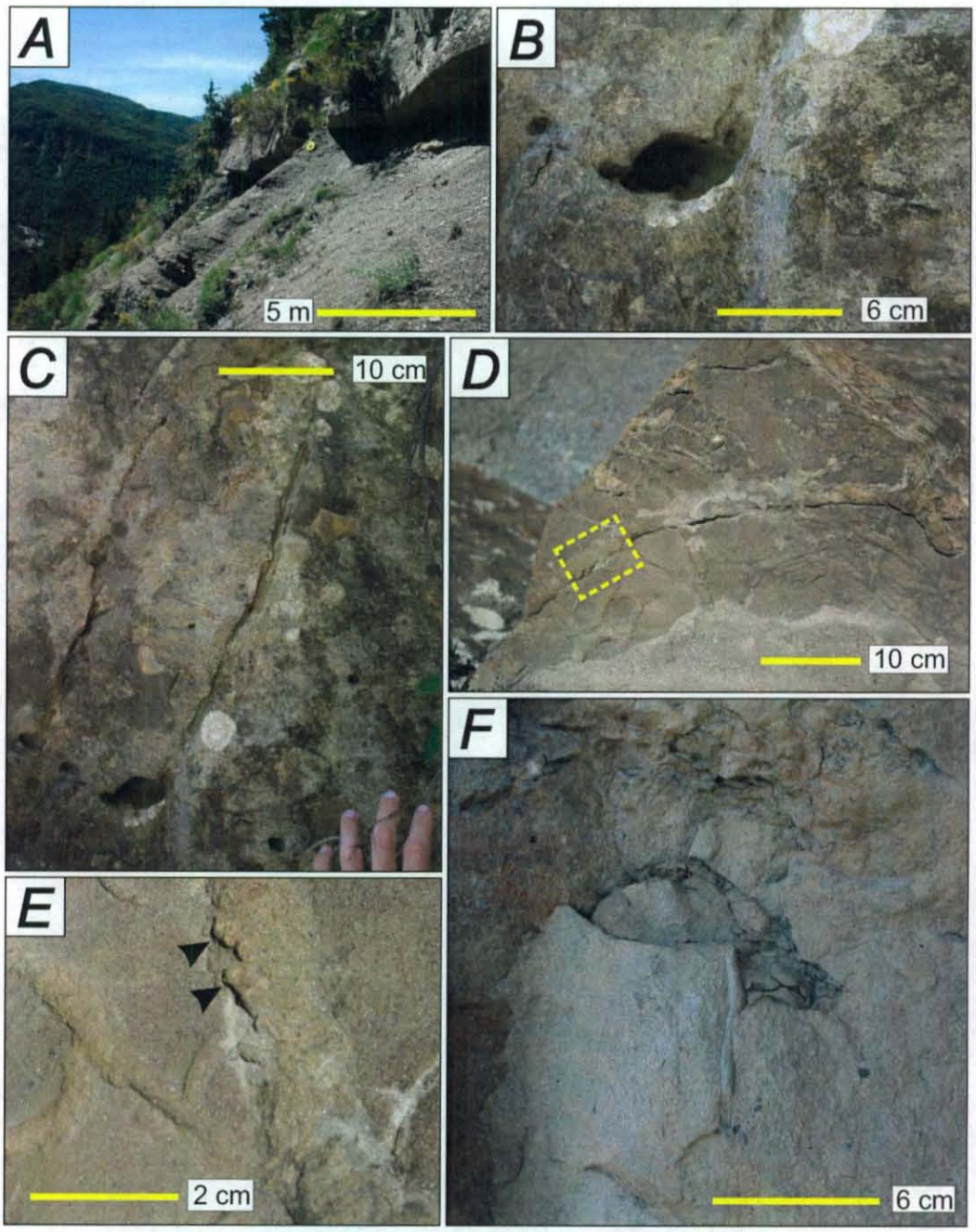


Fig. A5. Field image from the Argenton log. **A.** Transition from the Marnes Brunes Inférieures Formation to the Grès d'Annot Formation (thin-bedded turbidites to massive sand). **B.** Weathered out intraclast. **C.** Two *Ophiomorpha rudis* burrows heading towards previously silt/clay-filled intraclasts. **D.** Branched *O. rudis* on the top of sandstone turbidite with sandy pellets. **E.** Close up of the sandy pellets (arrowed) from inset in D. **F.** *O. rudis* burrow emerging from a silty intraclast and continuing vertically down.

APPENDIX B

Extended results of geochemical analysis

Explanation

Appendix B contains the results of the geochemical analyses presented in Chapter 3. Tank 2 was used for sampling as it had the most visually striking burrows with pelleted walls resembling *Ophiomorpha rudis*. Table B.1. lists the samples used for TOC and $\delta^{13}C_{org}$ analyses along with a brief description. The positions from within the tank are shown in a series of images overleaf on Fig. B-1. Sampling was done on a coordinate-based system. The tank had two mud layers, an upper (U) and a lower (U; Fig. B-1A). The tank was serially sliced. Eight slices (A to I) were made in the Z plane and sampling was done at each interval (Fig. B-1B). Samples of Slice A were sampled against the right wall of the tank (A = 0 cm). Samples taken during slice B were 10 cm in from the wall (B = 10 cm). Increments are shown in Fig. B-1B. Three positions are marked in the Y plane (1, 2, and 3). This made sampling easier, methodical, provided a naming system. Consequently, sample LC3 was taken from the lower mud layer at slice C3. *Neotrypaea californiensis* constructed a burrow against the wall of the tank (Fig. B-1C). In addition to the grid samples, samples of pellets and burrow linings were also taken from this burrow against the glass wall (labelled on Fig. B-1C). The raw geochemical data is then presented after on pages B-5 and B-6.

Sample Name	Description
BH1 BH2 BH3	Taken from the burrow floors of burrows in the lower mud layer.
BL1	Mud burrow lining
BS2	Burrow lining/pellets
BS4	Burrow lining/pellets
LC3	Unbioturbated material
UB2	Unbioturbated material
UF1	Burrow fill (backfilled material)
UG1	Pellets

Table B.1. Names and descriptions of the samples taken from tank 2. See text and Fig. B-1 for positions within the tank.

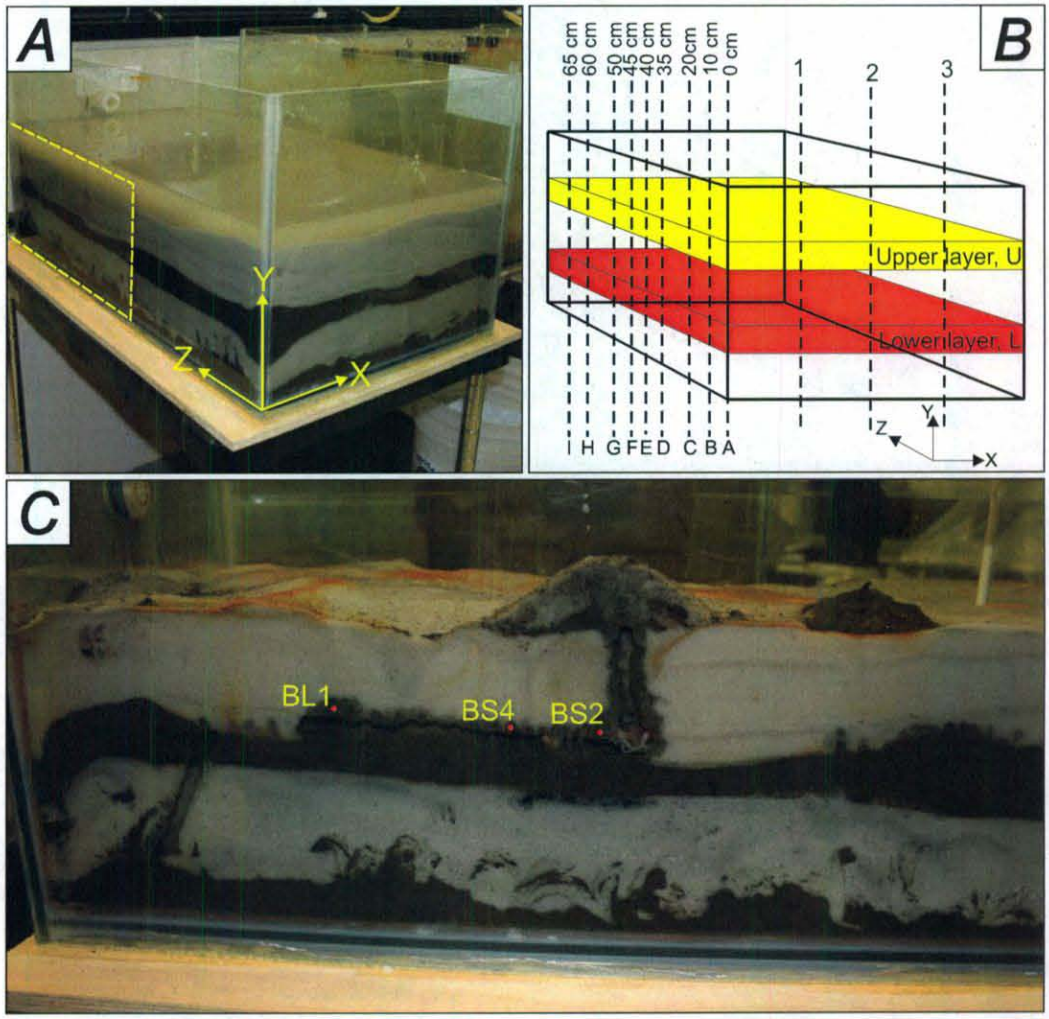


Fig. B-1. Images from tank 2 indicating the positions of samples taken for geochemical analysis. **A.** Set up of tank 2 with two mud layers. The X, Y, and Z planes are shown and relate to the schematic diagram to the tank in B. The dashed yellow box indicates the field of view of the images in C. **B.** 3-D representation of the tank showing the coordinates system used for sampling and naming. **C.** *Neotrypaea californiensis* in its burrow against the wall of the tank. Sample locations are shown.

DeltaVPlus-Carlo Erba: Carbon Isotope Analysis

Memorial University
CREAIT Network - TERRA Facility
Stable Isotope Lab

Run Date: March 3, 2010
Client: C. Phillips
Operator: C. Phillips, A. Pye
Isotope: $\delta^{13}C$

Please quote OurLabID when making enquiries a

OurLabID	Sample ID	Date Time	Analysis	Analysis Comment	Amount (mg)	Peak Amplitude (mV)	Delta of Peak	Mean Delta of All Analyses	StdDev of Deltas of All Analyses	%C for applicable media	Mean %C of All Analyses	StdDev of %C of All Analyses	Last Name	Submit Date
G-33	MUN-Sulfanilamide	03/03/2010	D-17814	primer	0.063	2241	-28.52	-28.57	0.06	38.26	42.96	4.18	Reference	26/07/2006
G-33	MUN-Sulfanilamide	03/03/2010	D-17815	primer	0.062	2665	-28.62	-28.57	0.06	46.27	42.96	4.18	Reference	26/07/2006
G-33	MUN-Sulfanilamide	03/03/2010	D-17816	primer	0.052	3067	-28.61	-28.57	0.06	62.79			Reference	26/07/2006
G-33	MUN-Sulfanilamide	03/03/2010	D-17817	primer	0.052	2228	-28.52	-28.57	0.06	44.35	42.96	4.18	Reference	26/07/2006
G-36	Blank capsule	03/03/2010	D-17818		0.000	133							Reference	26/07/2006
G-36	Blank capsule	03/03/2010	D-17819		0.000	123							Reference	26/07/2006
G-36	Blank capsule	03/03/2010	D-17820		0.000	133							Reference	26/07/2006
C-133	MUN-CO-2	03/03/2010	D-17821		0.195	2392	-40.07	-40.11	0.10	12.14	12.67	0.58	Reference	26/07/2006
C-133	MUN-CO-2	03/03/2010	D-17822		0.206	2568	-40.15	-40.11	0.10	12.21	12.67	0.58	Reference	26/07/2006
C-132	MUN-CO-1	03/03/2010	D-17823	not used in calibration	0.195	436	-22.92			1.46			Reference	26/07/2006
C-132	MUN-CO-1	03/03/2010	D-17824		0.194	2674	-21.02	-21.02	0.02	13.41	12.67	0.67	Reference	26/07/2006
G-35	B2153 low org sediment	03/03/2010	D-17825		0.642	1201	-27.61	-27.52	0.11	1.68	1.66	0.05	Reference	26/07/2006
G-35	B2153 low org sediment	03/03/2010	D-17826		5.034	8374	-27.50	-27.52	0.11	1.62	1.66	0.05	Reference	26/07/2006
G-2261	BH1	03/03/2010	D-17827		1.111	9569	-23.26	-23.26		8.44	8.44		Phillips	23/11/2009
G-2262	BH2	03/03/2010	D-17828		1.711	22166	-23.42	-23.42		11.75	11.75		Phillips	23/11/2009
G-2263	BH3	03/03/2010	D-17829		1.224	13687	-23.41	-23.41		10.61	10.61		Phillips	23/11/2009
G-2264	UG1	03/03/2010	D-17830		1.425	23542	-23.96	-23.96		14.78	14.78		Phillips	23/11/2009
G-2265	UF1	03/03/2010	D-17831		1.430	10060	-23.44	-23.44		6.79	6.79		Phillips	23/11/2009
G-35	B2153 low org sediment	03/03/2010	D-17832		0.198	476	-27.38	-27.52	0.11	1.60	1.66	0.05	Reference	26/07/2006
G-2266	LC3	03/03/2010	D-17833		0.869	7150	-23.50	-23.50		8.02	8.02		Phillips	23/11/2009
G-2267	UB2	03/03/2010	D-17834		0.993	9986	-23.54	-23.54		9.70	9.70		Phillips	23/11/2009
G-2268	BL1	03/03/2010	D-17835		0.705	558	-23.32	-23.52	0.28	0.57	1.10	0.75	Phillips	23/11/2009
G-2269	BS2	03/03/2010	D-17836		1.170	6260	-23.44	-23.44		5.22	5.22		Phillips	23/11/2009
G-2270	BS4	03/03/2010	D-17837		1.035	12340	-23.34	-23.34		11.40	11.40		Phillips	23/11/2009
G-35	B2153 low org sediment	03/03/2010	D-17838		2.463	4316	-27.44	-27.52	0.11	1.70	1.66	0.05	Reference	26/07/2006
G-35	B2153 low org sediment	03/03/2010	D-17839		7.924	13982	-27.54	-27.52	0.11	1.66	1.66	0.05	Reference	26/07/2006
G-35	B2153 low org sediment	03/03/2010	D-17840		1.273	2295	-27.68	-27.52	0.11	1.71	1.66	0.05	Reference	26/07/2006
C-133	MUN-CO-2	03/03/2010	D-17841		0.160	2207	-40.23	-40.11	0.10	12.99	12.67	0.58	Reference	26/07/2006
C-133	MUN-CO-2	03/03/2010	D-17842		0.241	3330	-39.99	-40.11	0.10	13.32	12.67	0.58	Reference	26/07/2006
C-132	MUN-CO-1	03/03/2010	D-17843		0.216	2829	-21.00	-21.02	0.02	12.51	12.67	0.67	Reference	26/07/2006
C-132	MUN-CO-1	03/03/2010	D-17844		0.161	2076	-21.04	-21.02	0.02	12.10	12.67	0.67	Reference	26/07/2006
G-2268	BL1	03/03/2010	D-17845		5.361	8914	-23.71	-23.52	0.28	1.62	1.10	0.75	Phillips	23/11/2009

DeltaVPlus-Carlo Erba: Carbon Isotope Analysis

Memorial University
CREAIT Network - TERRA Facility
Stable Isotope Lab

Run Date: March 17, 2010
Client: C. Phillips
Operator: D. Harazim, C. Phillips
Isotope: $\delta^{13}C$

Please quote OurLabID when making enquiries

OurLabID	Sample ID	Date Time	Analysis	Analysis Comment	Amount (mg)	Peak Amplitude (mV)	Delta of Peak	Mean Delta of All Analyses	StdDev of Deltas of All Analyses	%C for applicable media	Mean %C of All Analyses	StdDev of %C of All Analyses	Last Name	Submit Date
G-33	MUN-Sulfanilamide	17/03/2010	D-17952	primer	0.068	3468	-28.72	-29.01	0.70	52.35	46.11	4.88	Reference	26/07/2006
G-33	MUN-Sulfanilamide	17/03/2010	D-17953	primer	0.069	2902	-28.56	-29.01	0.70	42.10	46.11	4.88	Reference	26/07/2006
G-33	MUN-Sulfanilamide	17/03/2010	D-17954	primer	0.070	3338	-30.05	-29.01	0.70	47.61	46.11	4.88	Reference	26/07/2006
G-33	MUN-Sulfanilamide	17/03/2010	D-17955	primer	0.055	2396	-28.70	-29.01	0.70	42.36	46.11	4.88	Reference	26/07/2006
G-36	Blank capsule	17/03/2010	D-17956		0.000	134							Reference	26/07/2006
G-36	Blank capsule	17/03/2010	D-17957		0.000	130							Reference	26/07/2006
G-36	Blank capsule	17/03/2010	D-17958		0.000	129							Reference	26/07/2006
C-133	MUN-CO-2	17/03/2010	D-17959		0.183	2452	-40.08	-40.11	0.23	12.66	12.67	0.21	Reference	26/07/2006
C-133	MUN-CO-2	17/03/2010	D-17960		0.210	2850	-40.08	-40.11	0.23	12.82	12.67	0.21	Reference	26/07/2006
C-132	MUN-CO-1	17/03/2010	D-17961		0.182	2405	-21.15	-21.02	0.10	12.39	12.43	0.25	Reference	26/07/2006
C-132	MUN-CO-1	17/03/2010	D-17962		0.185	2398	-20.92	-21.02	0.10	12.13	12.43	0.25	Reference	26/07/2006
G-35	B2153 low org sediment	17/03/2010	D-17963		0.602	1202	-27.65	-27.46	0.13	1.75	1.64	0.10	Reference	26/07/2006
G-35	B2153 low org sediment	17/03/2010	D-17964		5.166	8992	-27.43	-27.46	0.13	1.64	1.64	0.10	Reference	26/07/2006
G-35	B2153 low org sediment	17/03/2010	D-17970		0.264	541	-27.29	-27.46	0.13	1.49	1.64	0.10	Reference	26/07/2006
C-133	MUN-CO-2	17/03/2010	D-17976		0.205	2807	-40.37	-40.11	0.23	12.88	12.67	0.21	Reference	26/07/2006
C-132	MUN-CO-1	17/03/2010	D-17977		0.248	3383	-20.93	-21.02	0.10	12.80	12.43	0.25	Reference	26/07/2006
G-35	B2153 low org sediment	17/03/2010	D-17978		2.532	4472	-27.44	-27.46	0.13	1.68	1.64	0.10	Reference	26/07/2006
G-35	B2153 low org sediment	17/03/2010	D-17984		7.920	14289	-27.47	-27.46	0.13	1.65	1.64	0.10	Reference	26/07/2006
C-133	MUN-CO-2	17/03/2010	D-17990		0.181	2461	-39.77	-40.11	0.23	12.66	12.67	0.21	Reference	26/07/2006
C-132	MUN-CO-1	17/03/2010	D-17991		0.204	2728	-21.10	-21.02	0.10	12.49	12.43	0.25	Reference	26/07/2006
G-2262	BH2	17/03/2010	D-17998	labelled STA0927	0.647	8444	-23.20	-23.20		12.35	12.35		Phillips	23/11/2009
G-2264	UG1	17/03/2010	D-17999	labelled G-2262	0.367	3890	-23.92	-23.92		10.05	10.05		Phillips	23/11/2009
G-2268	BL1	17/03/2010	D-18000	labelled G-2264	3.234	3346	-23.78	-23.78		0.98	0.98		Phillips	23/11/2009
C-133	MUN-CO-2	17/03/2010	D-18001	labelled G-2268	0.193	2560	-40.26	-40.11	0.23	12.33	12.67	0.21	Reference	26/07/2006
C-132	MUN-CO-1	17/03/2010	D-18002	labelled C-133	0.178	2365	-20.99	-21.02	0.10	12.33	12.43	0.25	Reference	26/07/2006

APPENDIX C
Publications

Below is a list of my publications at the time of final submission of this thesis.

McIlroy, D., Tonkin, N. S., Phillips, C. & Herringshaw, L. G. 2009. Comment on "*Ophiomorpha irregulaire*, Mesozoic trace fossil that is either well understood but rare in outcrop or poorly understood but common in core" by R. G. Bromley and G. K. Pedersen [Palaeogeography, Palaeoclimatology, Palaeoecology 270 (2008) 295–298]. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **284 (3-4)**, 392–395.

Phillips, C. & McIlroy, D. 2010. Ichnofabrics and biologically mediated changes in clay mineral assemblages from a deep-water, fine-grained, calcareous sedimentary succession: an example from the Upper Cretaceous Wyandot Formation, offshore Nova Scotia. *Bulletin of Canadian Petroleum Geology*, **58 (3)**, 203–218.

Phillips, C., McIlroy, D. & Elliott, T. 2011. Ichnological characterization of Eocene/Oligocene turbidites from the Grès d'Annot Basin, French Alps, SE France. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **300 (1-4)**, 67–83.